

On the Classification of Actiniaria.

Part II.—Consideration of the whole group and its relationships,
with special reference to forms not treated in Part I.¹

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With 20 Text-figures.

CONTENTS.

	PAGE
1. INTRODUCTION	493
2. BRIEF HISTORICAL SECTION	497
3. DISCUSSION OF CHARACTERS TO BE USED IN CLASSIFICATION	499
4. SPECIAL DISCUSSIONS AND OUTLINE OF NEW SCHEME	505
5. EVOLUTIONARY SUGGESTIONS	553
6. SUMMARY	566
7. SHORT GLOSSARY	572

1. INTRODUCTION.

It has been necessary, on account of the length of the present paper, to confine Part II to discussions; the definitions of families and genera involved, on the lines of those already given in Part I, will be printed in another issue of this Journal as Part III, which will also contain a list of literature and an index to genera covering Parts II and III. The list of literature will be additional to that printed in Part I, and any numbers given in brackets in the following pages will refer to the two lists as one whole.

Part I dealt with a relatively limited and compact group of

¹ Part I was published in Vol. 64 of this Journal.

anemones in a fairly detailed way ; the residue of forms is much larger, and there will not be space available in Part II for as much detail. I have not set apart a section of the paper as a criticism of the classification I wish to modify, as it has economized space to let objections emerge here and there in connexion with the individual changes suggested. Part I tried to clear the ground and discuss the method of attack, so that the arguments there given need not be repeated, and so that the general principle and method suggested there might be taken for granted in Part II. I should like to record here that in these papers on Classification there will be found points in contradiction to certain remarks in earlier papers—'Terra Nova' and 'Actinaria collected off Ireland'—but the point of view is bound to become modified in some particulars as further experience opens new vistas. That the view-point should remain immovably fixed in the light of developing knowledge would more need apology than that it should march with necessity. Work on Part II has served only to strengthen and confirm the plan suggested in Part I of this paper.

Definitions to be given in Part III are based as far as possible on anatomically-described species, leaving the more doubtful forms to fit themselves in as knowledge of them increases. Consequently lists of species given include rather the better-known forms on which the definition is founded, than exhaustive enumerations. Even to identify an anemone from an old figure or description is very risky ; to be sure of an old species one must obtain and re-describe the type-specimens if such exist. If there are none, it is guess-work—cf. Pax (75), p. 309, and others.

One result of working through all the Actinian genera (supported by a personal anatomical study of a large number of them) is the recurrence of impressions connected with the difficulty of species-identification of some of them from preserved material—and the unfruitfulness of the pursuit. It would seem that family and genus are fairly easily tracked down when once a certain number of data are gained, and that these are intelligible quantities. But when it becomes a matter

of species the variation of the different anatomical criteria of distinction may be so wide, and the limits of specific variation so little known, that to go beyond the genus is little more than guess-work ; especially when one thinks of the modification caused to certain characters by mode of preservation, degree of contraction or distension of the animal, age, reproductive condition, locality, and other things. Two paths there are here which need following. Firstly, a large number of anemones should be collected (some belonging to stable and some to unstable species, and representative of various families) in cases where it could be positively certified that all individuals collected for any one species were undoubtedly the same. These should be preserved in different ways and states, and a study made which would reveal the limits of specific variation—or it might prove that sometimes there are no limits. Even after this, many descriptions would need supplementing before a revision of species within the group could be attempted. The second path is the study of nematocysts ; it may prove that measurements of these will provide clear specific distinctions. I believe Professor Carlgren will bring forward a good deal of evidence in this connexion. I have not been able myself to give this point much attention, but what I have done rather suggests that the size of the cells is too variable and too similar in closely-related species to help us. Pax has a note on this in his paper on the 'Family Actiniidae', pp. 80-2. At least it becomes evident that species-identification from preserved material, with certainty, is going to be extraordinarily laborious. It would probably better repay effort to take more notice of the living animals, for here one's experience suggests that species-identification from colour and habit in life would usually be easy and sure. Experience is leading me to the view that among these low and plastic forms a species may have its peculiarities of organic constitution at an early stage of the development of their expression, such expression having affected colour scheme and general facies of the living animal but not necessarily to any extent the internal anatomy which can be studied in preserved

specimens. If this idea can influence the study of anemones, it will turn the attention of some workers in the direction of refuting it by minute research and measurement; and others towards 'leaving it at genera' and looking into the matters of living form and broader group-problems, in any case resulting in better knowledge of the group. Special detailed studies of individual families should yield good fruit. In some cases at least further work would reveal interesting and instructive similarities and variations running through all the members of a given family, but of a kind beyond the scope of the short definitions to which a paper like the present is limited. It would also reveal which families are more and which less homogeneous, and help to clear up ideas of relationships. I have made a preliminary study of the Chondractiniidae, for instance, which promises to be interesting in this sense.

Once more I wish to record hearty thanks to several friends who have given me their aid in one way or another, especially to Professor H. J. Fleure for much kindness, and to Captain A. K. Totton, M.C., for kind help with literature and specimens at South Kensington. I am also much indebted to Professor Stanley Gardiner for the loan of a collection of specimens without the aid of which it would have been very difficult to complete the paper.

Some of the illustrations in this paper are copied from other sources. Text-fig. 14, κ , is copied from Plate 22, No. 2, in W. Saville-Kent's 'The Great Barrier Reef of Australia' (W. H. Allen & Co., Ltd., 100 Southwark Street, S.E. 1); Text-fig. 19 is from a photo by Saville-Kent in 'The Naturalist in Australia', p. 224 (Chapman & Hall, Ltd., 11 Henrietta Street, W.C. 2), and later on printed in 'Marvels of the Universe', p. 1135 (Messrs. Hutchinson, Paternoster Row, E.C.); Text-fig. 9 is copied from 'Journ. Mar. Biol. Soc.', N.S., vol. x, no. 1, 1913, p. 73; Text-fig. 8 is from 'Sci. Trans. R. Dublin Soc.', ser. ii, vol. iv, 1889, Pl. 35, fig. 1. I wish to acknowledge with thanks permission to print my versions of these figures, from Messrs. W. H. Allen, Chapman & Hall, and Hutchinson, Dr. E. J. Allen, the Science Committee of the

Royal Dublin Society, and the executors of the late Mr. Saville-Kent.

2. BRIEF HISTORICAL SECTION.

Unfortunately space forbids the inclusion here of even outline histories of all the families dealt with in the paper similar to those given for Sagartiidae and Paractidae in Part I. The number of families is far greater, and possibly the historical interest is less than in the previous case. The following details, therefore, are limited to an outline of the more usual classifications used up to date, and which it is the suggestion of this paper to modify.

G. C. Bourne's scheme is the following :

Class ANTHOZOA.

Sub-class I. Octactiniaria (Octocorallia, Carlgren).

Sub-class II. Ceriantipatharia (Hexacorallia, Carlgren).

Sub-class III. Zoanthactiniaria (Dodecacorallia, Carlgren).

Order 1. Zoanthinaria.

Order 2. Edwardsiaria.

Order 3. Dodecaactiniaria.

Sub-order A. Madreporaria.

Sub-order B. Actiniaria.

The principle of his three sub-classes is that of Carlgren, Bronn's Thierreich, 1908.

The position of the Zoanthinaria and Edwardsiaria varies in different schemes. In Carlgren's 1900 plan, for instance, the Edwardsiaria go under his group Athenaria, and the Zoanthinaria stand away separately and rank equal to the Ceriantharia and Actiniaria. Bourne has recently shown (9) that the Edwardsiids must be clearly separated from ordinary Actinians, and it is his allocation of them which is to be accepted.

The subdivision of the sub-order Actiniaria will vary accordingly as one follows Carlgren or not. Carlgren's division, as used by him in 'Ostafrikanische Aktinien' (1900), for example, is as follows :

Sub-order ACTINIARIA.

Tribe 1. Protantheae.

Sub-tribe 1. Protactininae.

Sub-tribe 2. Protostichodactylinae.

Tribe 2. Nynantheae.

Sub-tribe 3. Actininae.

A. Athenaria.

B. Thenaria.

Sub-tribe 4. Stichodactylinae.

Other arrangements ignore the Protantheae and Nynantheae, dividing at once into Actininae and Stichodactylinae, in which case the Protactininae rank as Actininae, the Protostichodactylinae as Stichodactylinae.

The Protantheae are separated from the Nynantheae by the possession, usually, of an ectodermal muscle-sheet and nerve-layer in the body-wall and generally in the actinopharynx also; and in some of them by the absence of basilar muscles, and ciliated tracts on the mesenterial filaments. The Actininae and Stichodactylinae, and similarly the Protactininae and Protostichodactylinae, are marked off from each other by the fact that in the Actininae (and Protactininae) only one tentacle communicates with each exocoel and endocoel, at most, whereas in the other groups two or more tentacles grow out from at least the stronger endocoels.

This section may suitably contain a list of the more generally-used families, which will be convenient for reference later, assigned to their respective positions under Carlgren's main groups.

1. PROTAECTININAE: Gonactiniidae, Ptychodactidae, Halcuriidae.
2. PROTOSTICHODACTYLINAE: Corallimorphidae.
3. ACTININAE:
 - ATHENARIA: Ilyanthidae, Halcampidae, Halcampomorphidae, Andvaekiidae, Halcampactidae.

THENARIA : Sagartiidae, Paraactidae, Boloceridae, Actiniidae, Bunodidae, Aliciidae, Phyllactidae, Dendromeliidae, Minyadidae.

4. STICHODACTYLINAE : Discosomidae, Stoichactidae, Heteranthidae, Homostichanthidae, Aurelianiidae, Actinodendridae, Phymanthidae, Thalsianthidae.

This is, of course, the list as it stands without taking any account of the present paper, even Part I of it. The work of Part I was chiefly devoted to a revision of the Sagartiidae and Paraactidae, taking those names in the old sense as used on this page.

3. DISCUSSION OF CHARACTERS TO BE USED IN CLASSIFICATION.

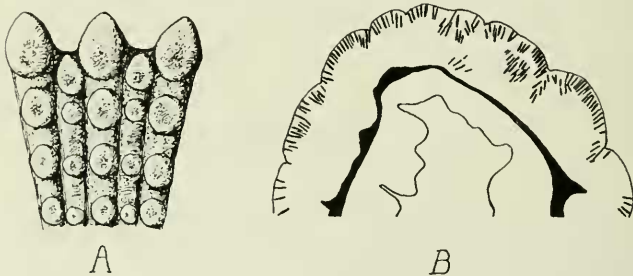
The characters already discussed in Part I, pp. 456-68, will of course be used here again, where they come in, but a few others remain to be mentioned.

In the families under discussion now, there are no mesogloal sphincters save in *Halcampa*, but it has to be decided how far the character of the endodermal sphincter is to be trusted as a family feature. All grades of it exist, from very weak diffuse or very weak circumscribed to very strong circumscribed, through various degrees of diffuseness and circumscribed diffuseness (cf. Text-figs. 11 and 12). It may be quite absent. In some families the range is not more than from absent to weak diffuse. But in other cases there are so many grades that one can draw no line of demarcation anywhere; and it must be admitted that the form and grade of development of the sphincter cannot be used as a family character except where it is fairly stable. The same thing really applies to mesogloal sphincters, but here it has been less noticed because no one happens to have suggested an artificial distinction between diffuse and circumscribed mesogloal sphincters.

It has long ago been realized that presence or absence of

verrucae and acrorhagi¹ cannot be used in limiting families, and this leads on to the question of vesicles. A certain number of forms develop, either all over their bodies or in certain parts only, various sorts of hollow vesicular outgrowths of the coelenteron (see Text-figs. 2, A, and 18). These may be slightly or very highly specialized. It may be argued that they are only verrucae which have gone farther, but in most cases they have gone a good deal farther, and really

TEXT-FIG. 1.



- A. Small portion of the upper part of the body of *Bunodactis alfordi*, somewhat enlarged, to show the vertical rows of verrucae, three of them ending above in conical acrorhagi.
- B. Half a transverse section of an acrorhagus of *B. alfordi*. Mesogloea black, ectoderm and endoderm white, the black strokes in the former representing nematocysts.

seem to constitute a definite and characteristic feature by which forms possessing them may be separated from those which do not. Since these forms also show an agreement among themselves in other ways, falling naturally into sets, we may fairly take 'presence of vesicles' as a family character for use among others.

The presence or absence of a definite base seems a valid

¹ In this paper the term 'acrorhagi' is used to cover 'marginal spherules' of any sort, whether simple or compound, whether nematocyst batteries or not. There seems to be too much variation in their structure for it to be possible to maintain a serviceable distinction of them into acrorhagi, pseudo-acrorhagi, &c. A sketch of typical acrorhagi from *Bunodactis alfordi* is given in Text-fig. 1.

and useful distinction between the Ilyanthids and the (more or less) adherent forms, even though in special instances the Ilyanthid condition is partly retained or imitated by others. Text-fig. 7 shows the contrast between the two states. The conversion of the base into a definite float as in *Minyas* provides a third useful type.

Among the forms without acontia or mesogloal sphincters one cannot make use of presence or absence of cinclides as might have been hoped. They have here excited so little interest that not much trouble has been taken to find them, and the range of their distribution is not really known. They are recorded in some forms such as *Peachia* and *Harenactis*, and I must record here that I have personally observed them very clearly in a species of *Phymanthus*—quite an unexpected find. It seems to me not unlikely, from noticing the ways of living anemones, that there may be discovered cinclides of some sort (even if only acrorhagial perforations) in some or even many families. A study of *Actinia equina*, *Anemonia sulcata*, *Bunodactis gemmacea*, and *Tealia crassicornis* in this connexion might reveal something quite interesting—and attention should be paid to the thin region just near the edge of the base, as well as to the rest of the body.

Among *Stichodactylines* we have to deal with characters of quite a clear-cut sort affecting form and arrangement of tentacles, and these provide simple and satisfactory family distinctions. (See Text-figs. 2, B, 14, 15, 19.)

Taking these remarks, together with the similar ones in Part I, we may list some of our more useful characters as follows :

Presence or absence of (i) a definite base, (ii) a float, (iii) cinclides, (iv) a distinction of the body into regions, (v) vesicles, (vi) a mesogloal sphincter, (vii) acontia, (viii) mesogloal disc-and-tentacle muscles, (ix) a division of the mesenteries into macro- and microcnemes, (x) macrocnemes over and above six pairs, (xi) perfect mesenteries over and above six pairs, (xii) more tentacles than one in connexion with some or

TEXT-FIG. 2.



- A. Vertical section of a whole specimen of *Phyllodiscus*, to show two vesicles (*v*) and two tentacles (*t*) cut through. Mesenteries, &c., are omitted for clearness. B. Vertical section of a portion of the upper part of the body-wall and outer part of the oral disc of *Cryptodendron*. The section passes through many short tentacles (*t*), and although all do not belong to the same mesenterial chamber (mesenteries are omitted for clearness), there is not by any means only one tentacle to each chamber as at A. *s*, sphincter; *b*, body-wall.

all of the endocoels, (xiii) more tentacles than one in connexion with some or all of the exocoels, (xiv) permanent tentacle-bearing arms of the oral disc.

This is of course an incomplete list, but other characters not needing special mention here will reveal themselves in their respective contexts. None of the characters can be treated in an absolutely hard-and-fast way, and may need special consideration in special cases. Of those listed, nos. iv and viii affect genera more than families, but are interesting even if their presence or absence does not in itself determine the fate of a given form. No. vi has to be taken in connexion with the fact that sphincterless forms have to be included sometimes with forms which have a mesogloal sphincter, sometimes with those possessing an endodermal one, or else alone, according to the sum of their other characters. Characters such as presence or absence of brood-pouches are not of much classificatory use.

There are many other things involved in classifying Anthozoa which will be pointed out in due course, but a few need special mention; they affect most, on the whole, groups larger than families. These may be taken one at a time.

(i) Presence or absence of ciliated tracts on the mesenterial filaments. These ciliated 'tracts' or 'pads' (Flimmerstreifen of German authors) are very definite structures, and their presence or absence seems to be one of the soundest indications we have of difference of tendency between one group and another. It forms also an easily-made-out character and one to which there is hardly any of the usual objection of intermediate conditions between presence and absence. Their loss, as I conceive it (or their non-development if it were that), by the corals and by certain anemones seems to constitute a very distinct evolutionary step, which may be seized upon for purposes of classification. Its usefulness both as a clue and as a sound distinction has been somewhat swamped by the amount of attention which the next character has absorbed; but I propose here to lay a good deal of stress upon it as being more valuable than no. ii. The

contrast between the kind of filament with ciliated tracts and that without may be seen from Text-fig. 17, where three of the four sorts of filament illustrated have the tracts (though not all the same kind of tract, in detail), and the fourth has none (c).

(ii) Presence or absence of ectodermal muscle in body-wall.—In this case we are dealing with a universal ancestral character which has been allowed to die out in most forms. It persists in those retaining most primitiveness, and is present, at least partially or as a vestige, here and there among more advanced forms, physiological causes probably accounting for its retention. It can therefore only be used in a limited way in a classification—useful in defining primitive groups, but not a criterion of relationship when it becomes a question of forms some of which have retained it, in greater or less degree, and others have shed it.

(iii) Presence or absence of spirocysts in ectoderm of body-wall.—This is another character about which a similar view may be taken to that developed in connexion with the last one.

(iv) Presence or absence of basilar muscles.—These muscles are natural developments correlated with the stabilizing of a well-marked basal disc. Their presence is certainly a good characteristic of the higher forms in general, but here again it may be misleading to think too much about them in connexion with transitional forms or forms of doubtful relationships. For purposes of family-definitions, it appears that the presence or absence of the base itself is the first consideration, basilar muscles or not.

(v) Presence or absence of any perfect metaenemes.—One set of forms (*Gonactinia*, *Protanthea*, and *Oractis*) seem well distinguished from others by virtue of the fact that they alone among Actinians (excluding Edwardsiids and odd individuals among *Halcampas*, *Aiptasias*, &c.) have the four couples of protoenemes (the eight 'Edwardsia-mesenteries') perfect, none of the metaenemes being so, with the result that there are no perfect

pairs. This, taken among other things, seems to mark them off pretty well from other primitives, and constitutes a character upon which one is inclined to lay more weight than has been done hitherto—it is another, though a less important one, the value of which has been somewhat overshadowed as in the case of the ‘ciliated tracts’, by the discussion of ectodermal musculature. A diagram showing this type of mesenterial arrangement for comparison with others may be found in Text-fig. 16, B.

4. SPECIAL DISCUSSIONS AND OUTLINE OF NEW SCHEME.

§ A. The Gonactiniidae.

This family has been made to include *Protanthea*, *Gonactinia*, *Oractis*, and *Boloceroides*. For purposes of this discussion we shall limit it to *Gonactinia* and *Protanthea*, with *Oractis* as a probable but insufficiently-known member. *Boloceroides* requires separate treatment. The *Gonactiniidae*, then, have in common a number of characters, most of them primitive. The smooth unspecialized body has a definite attachable basal end, but without any basilar muscles. The animal is small and delicate, and has both the inner and outer surfaces of the whole of its mesogloea covered by a weak generalized muscle-layer, not specially concentrated to form definite retractors or sphincters, and present in ectoderm of body-wall and actinopharynx as well as elsewhere. The body-wall ectoderm also shares the character of that of the tentacles in that it possesses spirocysts. The mesenterial filaments are without ciliated tracts, and only the first eight mesenteries to appear (i. e. the protoconemes, which arise as bilateral couples and not as pairs) are perfect (see Text-fig. 16, B). These undifferentiated forms seem to come nearer than any surviving thing to the probable ancestor of the *Zoanthactiniaria* (Text-fig. 16, A), which, whatever it was, must surely have had in common with them the small size and delicacy, the generalized musculature and generalized distribution of spirocysts, and the eight perfect mesenteries

only. Not only have the Gonactiniidae a good deal approximating them to this ancestor, but also there are no other forms of this grade which can fairly be placed in the same family with them. It seems that the family must be looked upon as one apart, and representative of past things; the remaining question, which will receive attention later, being the rank of the group to which it must be allocated.

§ B. *Boloceroïdes*.

This is a genus of uncertain affinities and needs unusually careful placing. Carlgren has thought of it as a Gonactiniid, and others as a Boloceroïd. It certainly does not come within the Gonactiniidae as understood in Section A, nor even near it. The characters by which it may be defined, those which most affect us at the moment, are as follows. (i) There is a definite base, but (ii) no basilar muscles. The body is (iii) smooth with unspecialized margin. (iv) There is no sphincter. (v) There is ectodermal muscle in the body-wall. (vi) Spirocyts are present in the body-wall ectoderm. (vii) The tentacles are deciduous. (viii) Six pairs of mesenteries are perfect. (ix) The mesenteries are not divided into macro- and microcnemes. (x) There are ciliated tracts on the filaments, but (xi) no true siphonoglyphes.

Of these characters, the genus shares nos. i to vi and ix and xi with the Gonactiniidae. Character vii turns up also in *Bolocera* and *Bunodeopsis*, and need not trouble us, because it is a special feature which may be taken as a convergence—not necessarily a token of relationship with *Bolocera*, and certainly not with *Bunodeopsis*. Characters viii and x are the two of importance in which it differs from the Gonactiniidae, but they are rather fundamental. *Boloceroïdes* represents a different stage altogether, by its possession of ciliated tracts and its attainment of pairs of perfect mesenteries, although at the same time it retains several primitive traits. It shares five characters (i, iii, viii, ix, x) with the genus *Myonanthus* (a form which, as will be seen, requires special consideration), but

differs from it in six others. It becomes evident that if we treat the sum-of-the-characters principle woodenly and mechanically here, we shall run *Boloceroïdes* into the *Gonactiniidae* or near them; but that will not represent the truth. It is a case for weighing individual points, and the best we can do for the genus is to place it near *Myonanthus*. Opinion will differ as to the relative value of the various points, but taking the general line of this paper, nos. viii and x will count more heavily for its relationship (not close) with *Myonanthus* than all its points of similarity to the *Gonactiniids*. For, after all, most of those points may be summed up as aspects of one fact, the generalized nature of the structure; they are primitive features not shed, and these are more numerous than usual outside the *Gonactiniidae*. There are other forms with much clearer relationships which retain some of them, e.g. *Bunodeopsis*.

This means the inclusion of *Boloceroïdes* either in the same family as *Myonanthus*, or in a family to itself near the one containing the latter. Some of its differences from *Myonanthus* are of generic importance only (deciduous tentacles and lack of sphincter), and the question remains whether its ectodermal muscles and spirocysts in the body-wall, and its lack of basilar muscles and siphonoglyptes can separate it. Considering the fact that in other coherent families some at least of these things may be present or absent, it leaves the separation a matter of doubt. In the present paper, therefore, *Boloceroïdes* will be included in the *Myonanthidae* (see pp. 524, 545, 564, &c.), with the reservation that probably there would be no harm in having a separate *Boloceroïdidae* (under *Endomyaria* and next to *Myonanthidae*) if preferred. The genus is evidently a transitional one.

Any close relationship between *Boloceroïdes* and *Bolocera* seems a matter of doubt. *Bolocera* may well be a subsequent development of the same stock, which has attained larger size and, with this, numerous perfect mesenteries, retiring to deeper water and losing the primitive condition of body-wall, &c. This, however, is no argument for

placing *Bolocera* with *Boloceroides*, but is additional evidence for thinking of the former as an Actiniid, taking the view that will be developed below, that the Actiniidae are one of the next steps on from the Myonanthidae.

I am conscious that the arguments used in this section are rather dangerous, and that along some such line an attack might be developed upon the whole system of classification by summation of characters. But I feel that it is a special case, like one or two others, and that, as suggested in Part I (p. 470), the summation principle must not be used blindly like an arithmetical measure; looking upon it as useful typically, but needing modification here and there.

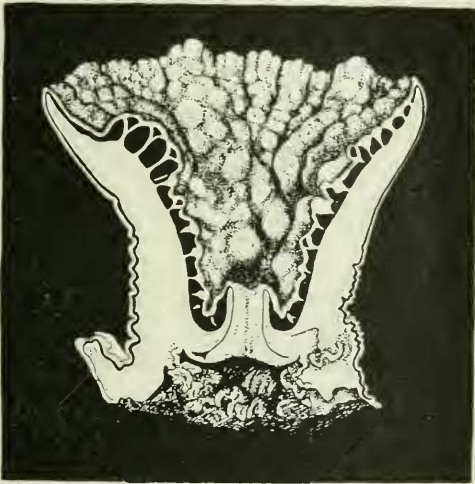
§ C. The Ptychodactidae.

Carlgren (1911) has shown clearly that two curious genera, very different in detail but similar in fundamentals (*Ptychodactis* and *Dactylanthus*), should be thought of together as forming one family. The debatable ground here is as to where the family fits into the general scheme. Carlgren includes it in his Protantheae with the Gonactiniidae. That the Ptychodactidae must be kept apart from the ordinary Actinians is pretty clear; also that they must come next to the Gonactiniids in a list. But apart from this general location, they seem to have very little to do with the Gonactiniids, and should be marked off from these by being placed in a group of their own and of higher rank than a family.

Of primitive characters they share with Gonactiniids the following: absence of basilar muscles although there is a base; similarity of structure between tentacles and body-wall—spirocysts and ectodermal muscle in both; sphincter little or none; mesenterial musculature weak, hardly forming retractors. They have no ciliated tracts on the filaments. On the other hand they have diverged from the Gonactiniids as regards size—they can get quite large—and have attained not only pairs of perfect mesenteries but often a good many of them. *Ptychodactis* has become very broad and has almost lost its actinopharynx (a unique case), and has numerous tentacles

and mesenteries. *Dactylanthus* has a good actinopharynx but has tentaculiform outgrowths of the body, curious actinopharyngeal pouches, and a fusion of the lower ends of the mesenteries into a columella-like network. Further, both genera are unique in two ways: firstly, the upper extremities of the filaments of the imperfect mesenteries are modified into curious structures like bisected funnels, the analogy of which

TEXT-FIG. 3.



One-half of a specimen of *Paradiscosoma*. Note the cup-shaped form, mouth on a cone at the bottom of the cup, tentacles reduced to knobs lining the cup. Mesogloea, &c., black. The base was injured, and is not fully shown. The tentacles have narrow 'stems' running through the thick mesogloea of the disc.

among other forms it would be difficult to suggest; and, secondly, the gonads and filaments are confined to different parts of each mesentery, the free border of the latter (or what corresponds to it in *Dactylanthus*) being occupied by filament above and gonad below, quite an unusual state of affairs.

From this one would judge that the Ptychodactids are a collection of curiosities which have diverged along a little

line of their own. Since they are in some ways primitive we may place them next to the Gonactiniids for convenience ; but because of their peculiarities they should be kept sufficiently apart from those to represent a quite distinct evolutionary line. The exact rank of the group Ptychodacteae which I propose for their reception will be better discussed in other sections (see pp. 540, 552, 554-6, &c.).

§ D. The Corallimorphidae and Discosomidae.

There has been a growing feeling among those who have worked at anemones that there is a good deal of inter-relation between them and the corals, and that we can no longer insist on a separation of them based on presence or absence of a skeleton alone. This feeling has been best expressed by Duerden (120) in a study of the Madreporarian relationships of certain Stichodactyline. Perhaps in this connexion too little attention has been paid to the soft parts of corals. We are undoubtedly justified in retaining two groups, Actinaria and Madreporaria ; but the justification is to be found in the sum-of-the-characters principle, and not in the presence or absence of skeleton merely. The reservation is, that if we maintain these two groups we must include in the Madreporaria some forms without skeleton. I am not familiar enough with Madrepores to generalize about them, but am relying on the details given in Duerden's paper—from which I gather that there are certain aspects of their soft parts which present a fair degree of uniformity through the group. With the Actinaria, as hitherto limited, this is not the case ; but if certain forms were removed from among them it would be so to a more reasonable extent. There are two families of forms, hitherto called anemones, which have all the characteristics of coral-polyps save a skeleton—in fact which are corals but for that one thing. If these two families be removed from the Actinaria and placed under Madreporaria in some way, the division into anemones and corals at once becomes more intelligible, and various difficulties disappear. The families in question are the Corallimorphidae and Disco-

somidae,¹ both 'Stichodactyline'. One advantage of placing these with the corals is that they are not like the remaining true Stichodactyline, which apart from them form a harmonious group (see p. 533).

Two further points arise: (i) are there any corals with the Stichodactyline arrangement of tentacles? and (ii) to which Madreporarian families do our forms most nearly approach? With regard to the first it does not much matter, for a Stichodactyline condition of tentacles could arise as a convergence anywhere, and has done so among the Ceriantharia. As to the second it is for a coral expert to suggest, and pending further investigation the families should simply go under Madreporaria without closer allocation.

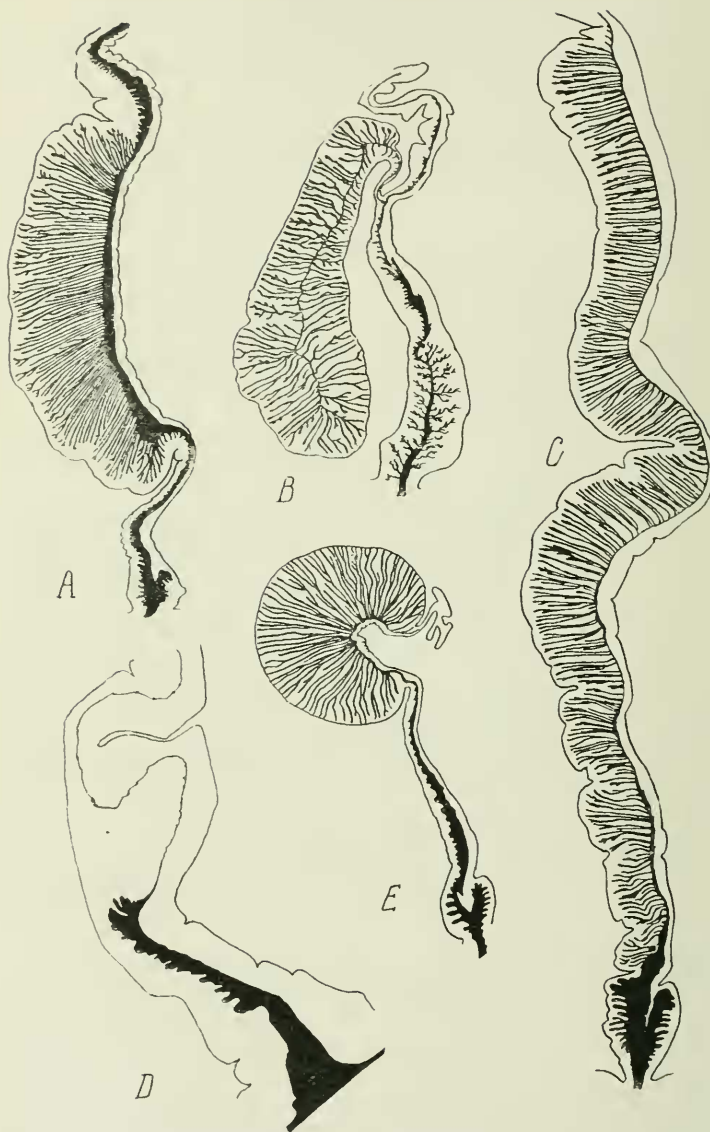
A vertical section of one of the animals in question is shown in Text-fig. 3. It is a cup-shaped form in which the tentacles have become reduced to mere knobs.

What are the points which make these forms like corals? A general statement about them might be made as follows:

They secrete no horny or limy skeleton. They may be quite solitary, or quite gregarious, sometimes living in sheets or carpets. Frequently they reproduce by fission, and often compound individuals with several mouths, or individuals connected by a basal coenosarc are found. The base is adherent. The body is without verrucae, variable in form and consistency. More than one tentacle connects with at least the older endocoels. The tentacles may be simple, or capitate (cf. *Caryophyllia* and others among corals), or branched; or small and wart-like, or even reduced to so little as to be invisible externally. There are no siphonoglyphes (or rarely?). The mesenterial filaments have no ciliated tracts. Sphincters are feeble or absent. Sting-cells of a size characteristic of Madreporaria, but not of Actinians in general, are usually found somewhere in the body. There are usually a good many

¹ The Discosomidae as referred to in this connexion means the family taken in Carlgren's sense, 1900, p. 58, and not in the wider sense of some authors—including only the genera *Discosoma*, *Paradiscosoma*, *Actinotryx*, *Rhodaetis*, *Orinia*, and *Ricordea*.

TEXT-FIG. 4.



Transverse sections of mesenteries, to show various types of musculature. Mesogloea black, endoderm white. A, *Epiactis*; B, *Aureliania*; C, *Cryptodendron*; D, *Actinotryx*; E, *Phymanthus*.

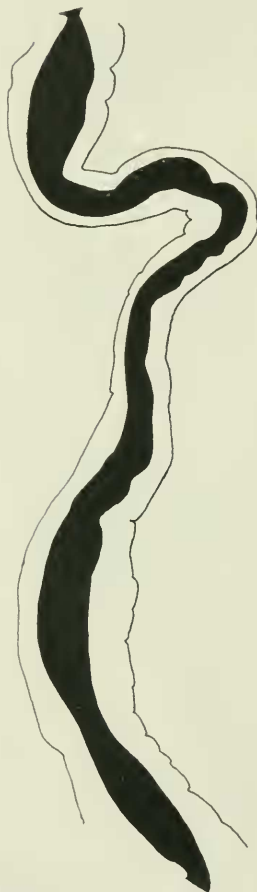
perfect mesenteries, and no distinction of mesenteries into macro- and microcnemes. The longitudinal mesenterial muscle consists typically of a feeble layer, not forming the sort of sheet or retractor characteristic of anemones. There are no basilar muscles, and directives may be present or not. The ectoderm of the body-wall may or may not contain a weak muscle-layer. The mesogloea is Madreporarian rather than Actinian.

Text-fig. 4 shows the contrast between various sorts of Actinian mesenterial musculature and the sort of thing found in these 'soft corals'. In the former there may be seen dendrites or processes projecting from the general mesogloea for the support of the muscle-fibres. In the soft corals the surface of the mesogloea is typically either straight or lobed as at D, but has a weak fringe of muscle-fibres directly upon it, not elevated on processes. The sort of thing is better seen in Text-fig 5. Text-fig. 6 shows Discosomid sting-cells contrasted with typical Actinian sting-cells from acontia and acrorhagi, &c. The general difference in size between A and B ('soft corals') and the others is very marked. C is unusually large for an Actinian cell, D and E providing more average examples. A Discosomid filament, showing the absence of ciliated tracts, is to be seen in Text-fig. 17, c.

A microscopical study of a few of these forms at once suggests a difference from the anemone type running through the histology and other things. Even when anemones have weak musculature it has a different appearance. These are things which one cannot well bring out in figures without an extensive histological demonstration, but are easy to see in actual sections. The curiously feeble mesenterial musculature, the presence of very large sting-cells, the absence of ciliated tracts, the appearance of the mesogloea and cell-layers, the lack of siphonoglyphes, the tendency towards compound individuals and colonies, the weak or absent sphincters, and sometimes the strong permanent actinopharyngeal ridges and form of the tentacles, and so on, are points which, taken together, suggest Madreporaria, of some or all of which they

appear, generally speaking, to be characteristic. One or other of them may be found among anemones, but their com-

TEXT-FIG. 5.

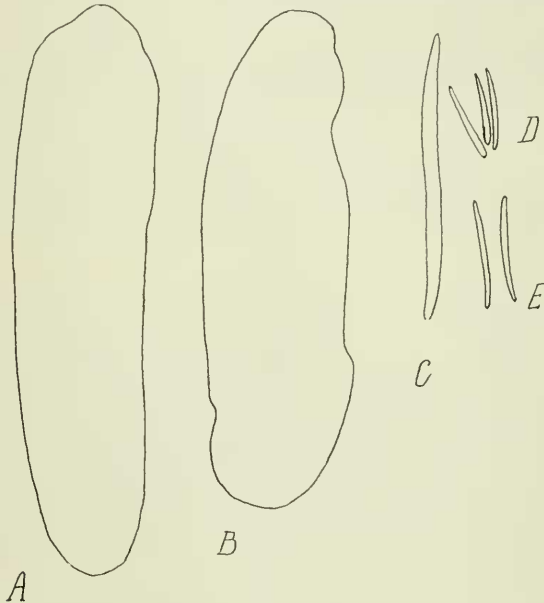


Transverse section of a mesentery of *Paradiscosoma* treated in the same way as those in Text-fig. 4. Note the heavy mesogloea (black) and absence of muscle-processes.

bination indicates coral affinities. Their distinctness from anemones in general struck me decidedly, before I thought of them as corals.

The presence of ectodermal muscle-fibres in the body-wall of *Corallimorphus*, &c., is doubtless a survival. Whether the weak general musculature is primitive in this case it would not be safe to say; there is much to suggest that it is a well-established thing here. Some of the other characters

TEXT-FIG. 6.



Sting-cells. All are drawn to same scale, as seen with $\frac{1}{6}$ objective and no. 3 ocular. A (*Actinotryx*) and B (*Paradiscosoma*) show the size characteristic of many 'soft coral' sting-cells. C is an unusually large Actinian cell from acontium of *Artemidactis*, and D (acrorhagi of *Bunodactis alfordi*) and E (*Halcampa aspera*, body-wall) show a more average Actinian size.

suggest advancement—the tentacles and their specialization of form and arrangement, the big sting-cells, numerous perfect mesenteries, and the sometimes thick and rigid bodies. The condition of mesenterial filaments they share with all corals. Taking them all in all suggestion of primitiveness here would

be much less safe than in the case of Gonactiniidae or even Ptychodactidae.

The Actiniaria as freed from extraneous skeletonless corals show general tendencies towards more complex individuality rather than towards colonial development, towards a special development of musculature in some way or another, towards different histology and on the whole more activity. They go in for expression of permutations and combinations of various characters, leading to great diversity—this diversity affecting differences among polyps, whereas it is perhaps more connected with variation of skeleton and colony-form, among corals, which may to some extent be compared with the Aleyonaria, although of course the latter much surpass them both in uniformity of the individual and diversity of the colony.

§ E.

The discussions so far have dealt with curious forms which, whatever their fate, are special cases, coming outside the main mass of anemones. Those that follow are concerned with forms the general position of which is fairly clear, i. e. they all come under the main tribe (Nynantheae in the sense taken on p. 540) of the sub-order Actiniaria, excluding Edwardsians, Zoanths, Gonactiniids, Ptychodactids and corals whether hard or soft—or to put it another way, they are presumably the descendants of a muscular *Halcampa*-like stage (cf. Text-fig. 8) with ciliated tracts on its filaments. Among these forms there seem to be four main sets which can be followed, and in the following sections the exceptional sets will be considered before the majority-forms.

§ F. The Ilyanthidae.

There has been a family Ilyanthidae in use for a long time ('*Actinies pivotantes*'), for the more or less vermiform creatures with no adherent base. It has been subdivided somewhat arbitrarily—that it needs subdivision is not in question, but how to do it. Although, however, we are obliged

to have more than one family, it seems wise to retain the old plan to the extent of having a group to cover them, the principle of which is good. This group must be labelled by Carlgren's name *Athenaria*, with the Edwardsiids of course excluded. The rank of this group will be discussed in a later section, but here we may consider the general characters justifying it.

The *Athenaria* appear to be the representatives of those forms which, being the outcome of a muscular *Halcampa*-stage, have retained more similarity to their ancestor than the majority of other forms, and have kept to a more or less burrowing life. There is variation in size; the predominating shape is vermiform, the relation of length to diameter varying in different cases and different states of expansion, diameter sometimes considerable. Text-fig. 7 shows the contrast between some of these and one of the ordinary adherent anemones with short wide form. In these *Athenaria* the aboral end is not a definite base, but a rounded physa, which is sometimes able, however, to adhere to small objects. There is little or no splincter. Often there are cinclides. The number of tentacles is usually small, and at most does not pass about forty. The number of mesenteries is similarly limited, and either these all have the grade of macrocnemes, or else there is a division into macro- and microcnemes—and in *Peachia* the state of affairs is intermediate. The mesenterial filaments have ciliated tracts.

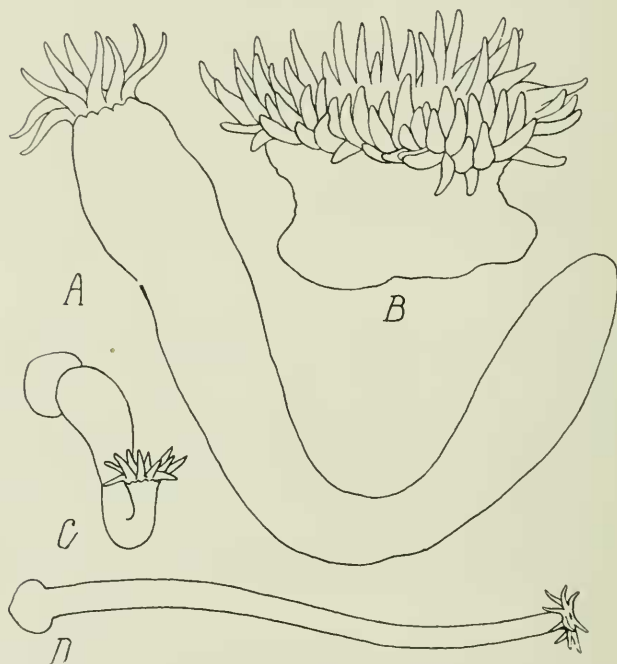
The above may be taken as a sort of definition of the burrowers or *Ilyanthlids*. The subdivision of the group remains to be discussed.

Of course, some of the forms formerly included here have long since been removed, others more recently—the *Ceriantharia* and *Edwardsiaria*. Forms with no base but with acontia are little known, but seem to fit in quite well with the *Phelliidae* (see Part I, p. 524), though possibly a new family may later on be needed for them. Carlgren has suggested a *Halcampactidae*, but it is here treated as coming under *Phelliidae*. *Andvackiidae* is not yet established. For *Halcampactis* see Part I, pp. 499, 509, 525.

The forms we are here concerned with are *Halcompa*, *Halcompoides*, *Pentactinia*, *Scytophorus*, *Har-enactis*, *Eloactis*, *Peachia*, *Haloclava*, *Ilyanthus*, and *Andresia*.¹

If we go into detail about all these forms we shall find that

TEXT-FIG. 7.



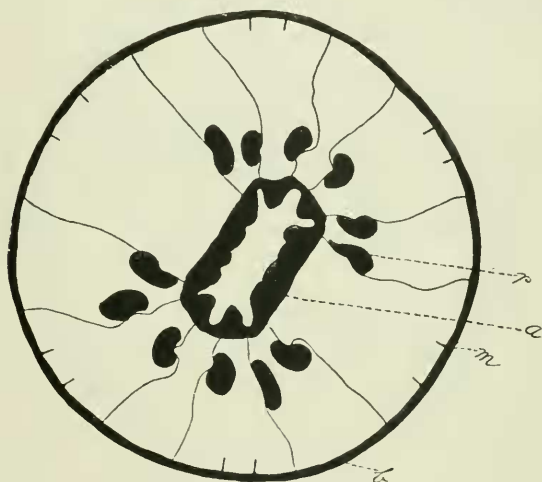
A, *Peachia hastata*; B, *Tealia crassicornis*; C and D, *Halcompa chrysanthellum*. To emphasize the contrast between burrowing and adherent forms. All are natural size.

almost every one could claim distinction for one reason or another; because there is diversity in rather important ways. But it would seem extravagant and hardly justifiable to give a family to each, and failing that we have to do the best we

¹ *Andresia* is a new name for *Ilyanthus parthenopeus*, which is quite unlike the more typical British *I. mitchelli*, and has to be separated as a distinct genus with new name. This will be formally established in Part III.

can, allowing a fair latitude of definition. It is possible to gather them into three fairly clear sets, which must be our families. It seems impossible to be content with a subdivision which has already been suggested, and based on the nature of the sphincter only—into Halcampidae, Halcampomorphidae, and Ilyanthidae. This, among other things, means that *Halcapa* and *Halcampoides* go into different families, and this seems to be straining things.

TEXT-FIG. 8.



Transverse section of *Halcapa chrysanthellum*, showing six pairs of macrocnemes and six pairs of microcnemes. *a*, actinopharynx; *b*, body-wall; *m*, microcneme; *r*, retractor. (After Haddon. See acknowledgement on p. 496.)

Taking first the genera *Halcapa*, *Halcampoides*, *Pentactinia*, and *Scytophorus*, we can make for these a fairly precise definition, and call them Halcampidae. They are Athenaria of more or less vermiform shape, with or without suckers or papillae or cuticle or incrustation on the body. There may be cinclides in the physa. The tentacles may be 8-12, 14, 20, or more, and their longitudinal musculature is ectodermal. The sphincter is absent, or weak endodermal, or weak mesogloal. The mesenteries have as their

main feature six pairs of macrocnemes ; but there are variations ; the full six pairs may not be developed (*Pentactinia* and some individuals of *Halcaampa*), or there may be an extra couple (*Scytophorus*). Microcnemes may be present or not.

This idea regards the genera *Halcaampa* and *Halcampoides* as constituting, jointly, types of the family, and no separation of these on account of sphincter is wise. It brings in *Pentactinia* and *Scytophorus*, the one as a slightly under-developed, the other as a slightly over-developed, *Halcaampa*-form. Indeed, these two are very like *Halcampas* but for mesenterial oddities slightly deviating from type. A case parallel to that of *Pentactinia* is that of *Decaphellia*, a *Phelliid* with subnormal number of macrocnemes. Text-fig. 8 shows a transverse section of a *Halcampid* for contrast with that of one of the *Ilyanthidae* in the strict sense as described in the next paragraph and illustrated in Text-fig. 9.¹

If we now take the genera *Ilyanthus* (*mitchelli*), *Harenaetis*, *Eloactis*, *Peachia*, and *Haloclava*, we find a rather different type of structure. The mesenteries are never fewer than ten pairs in adult animals, and vary up to about eighteen pairs. They all have virtually the grade of macrocnemes, even though there may be differentiation among them—except that in *Peachia* some of them are devoid of filament and gonad, but have strong retractors and are not microcnemes. For the rest they often attain fair size and may have stout bodies (capable of becoming vermiform) or very long ones. Suckers present or absent. Cinclides may occur. Tentacles simple or capitate, eight, twelve, twenty, or more, up to about forty. Little or no sphincter. There may be only one siphonoglyphe, which in *Peachia* is specialized into a conchula. In *Peachia* we have six perfect pairs of mesenteries (or rarely fewer?) and four secondary pairs ; in

¹ In this figure the gaps in the mesenteries are due to the fact that the section passes through the region of mesenterial stomata—in most regions the mesenteries would be continuous.

Eloactis and Haloelava ten pairs, all perfect; in Harenactis twelve pairs in two cycles, all perfect; in Ilyanthus the number of mesenteries varies, but is the same as the number of tentacles, and all are perfect—but there are some individual peculiarities as well.

Unless there is to be much multiplication of families the above arrangement seems the best.

TEXT-FIG. 9.



Transverse section of *Eloactis mazeli*. The gaps in some of the mesenteries are due to mesenterial stomata. Ten pairs of macrocnemes and no microcnemes. *a*, actinopharynx; *b*, body-wall; *r*, retractor. (After O. M. Rees. See acknowledgement on p. 496.)

There remains the case of *Ilyanthus parthenopeus*—or *Andresia parthenopea* as it must now be called. This form does not seem to fall in well with the usual idea of Ilyanthid structure, apart from its form and rounded aboral end. It has long tentacles in four regularly-graded cycles, and twenty-four pairs of mesenteries in three graded cycles. The mesenterial musculature appears to form only a weak layer, not rising into a thick (and typically circumscribed)

retractor or pad as in all other Ilyanthids. The body-margin is notched in a way suggestive of acrorhagi. In fact, but for its burrowing habit and rounded end, it would be a typical member of the Actiniidae of the less muscular sort. Whether it is an Ilyanthid which has passed the usual grade of development and moved towards that of adherent forms, or whether it is a retrograde adherent which has gone back to buried life and lost its base, we cannot tell. But in classification it ought to be separate, or probably go nearer the early Actiniids than the Ilyanthids. I have in this paper made a family Andresiidae for it, placing this among the earlier Endomyaria (see Part III).

With regard to other forms without bases excluded from the Athenaria (see Part I) these fit in better with the Mesomyaria (see pp. 541, &c.) than with the Athenaria, because of their acontia and mesogloecal sphincter, &c. In the case of some of them (Phelliidae in part) we have our finger on the transition from burrowing to adherence, and there are grades from a physa to a well-marked base; and as these seem to be getting up to the attached stage it seems better to keep them out of the Athenaria, especially since their acontia and mesogloecal sphincter and other things show their relationship to be with the Mesomyaria. Some of the Diadumenids are also almost without base, but here it is obviously a case of retrogression or arrested development; they are probably normally adherent forms changing under special conditions.

§ G. The Endocoelactids.

These forms start from a six-pairs-of-muscular-mesenteries or *Haleampa*-stage basis, with ciliated tracts on the mesenterial filaments, but work onward from this in quite an unusual way. The secondary mesenteries appear in the endocoels of the lateral primaries, and all of them have the character of directives (i.e. the retractors of each pair face away from one another). The usual plan is, of course, for the secondaries to appear in the primary exocoels, and have their retractors *vis-à-vis*. The contrast is indicated in Text-fig. 16, *g* being an Endocoelactid. Apart from this most fundamental structural

aberration, the Endocoelactids are sphincterless, and nearly always have spirocysts in the body-wall ectoderm. There is a definite base. The form of body and tentacles is variable, and may be ordinary, but the wall may be thick and heavy, the disc lobed, the tentacles often with aboral basal swellings. In fact we find here a tendency not found on the main line of Endomyaria (see p. 541, &c.) or 'endodermal-sphinctered' anemones, towards a deep-water specialization similar to that which we found earlier on in certain Paractids and Actinocyphids, &c. (see Part I). Taking them as wholes, the Endocoelactids are a set very different from average forms, being apparently a little line of evolution to themselves; and as such they should have slightly higher rank than that of a family, forming a group Endocoelactaria equal in level to the Athenaria.

Carlgren includes Endocoelactids in his Protanthæae along with Gonactiniidae and Ptychodactidae; but since they seem evidently derived from a muscular *Halcampa*-like ancestor with ciliated tracts, and have no ectodermal muscle in their body-walls, I cannot see the merit of that plan, or accept it. (See also pp. 541-2, 560, &c.)

There are among the Endocoelactids two rather clearly marked out groups, one of them containing *Halcurias* and *Carlgrenia*, the other *Actinernus* and three related genera. The two groups seem to have fairly good claims to be regarded as families, and as such they are defined later on in this paper (Part III). There is in one of the families practically a division of the mesenteries into macro- and microcnemes (macrocnemes six to ten pairs, with circumscribed retractors, gonads, and filaments; microcnemes confined to upper part of body except for four pairs of them in *Carlgrenia*—some of them may be perfect, but without retractor, gonad, or filament), and also there is constantly one siphonoglyphe only and no tendency to lobing of disc or tentacles. These forms, especially *Carlgrenia* (Text-fig. 16, c), are nearer their *Halcampid* ancestor than the others. In the other family we find the lobing tendency and charac-

teristically thick body-walls, two siphonoglyphes, and numerous mesenteries, the older ones at least fertile and not much marked off from the others, many being perfect and their musculature not strong. The first family is the Haleuriidae sens. strict., the second the Actinernidae.

§ H.

The next five sections will deal with the 'Sea-Anemones' in the narrowest sense (i.e. such of them as were not dealt with in Part I), the usual forms, the majority-forms, exclusive of atypicals such as Athenaria and Endocoelactaria and the pre-Halcampid groups.

§ J. The family Actiniidae.

This family, containing our commonest and most familiar anemones, has been the subject of a good deal of discussion and fluctuation. As it is usually understood at the moment, it is not much more homogeneous than the old group 'Paractidae', but contains three distinct types of mesenterial arrangement. Any discussion of it involves also the families Boleridae and Bunodidae, and these points will be dealt with in order.

Firstly, the Actiniidae. If we consider the aggregate of genera usually included here—*Actinia*, *Anemonia*, *Condylactis*, *Gyrostoma*, *Actinioides*, *Condylanthus*, *Myonanthus*, *Macrodaetyla*, and others, we find three types of mesenterial formula, as follows :

(i) In *Condylanthus* the mesenteries are divided into macro- and microcnemes, the macrocnemes numbering six pairs (cf. Text-fig. 16, c).

(ii) In *Myonanthus* and *Macrodaetyla* there is no division of mesenteries into macro- and microcnemes, but only six pairs are perfect (cf. Text-fig. 16, d).

(iii) In the others there is no division of mesenteries into macro- and microcnemes, but there are numerous perfect mesenteries as a rule, always more than six pairs in adults (cf. Text-fig. 16, u, and Text-fig. 10).

Without going over the old arguments again, we take it that if the ideas advocated in this paper be accepted at all, it will have been made clear in Part I that forms exhibiting these grades of mesenterial development need separation. We have, therefore, at once three families, Condylanthidae, Myonanthidae, and Actiniidae sens. strict., and these will be defined in Part III. This gives a homogeneous and intelligible Actiniidae, and has the advantage of providing two

TEXT-FIG. 10.

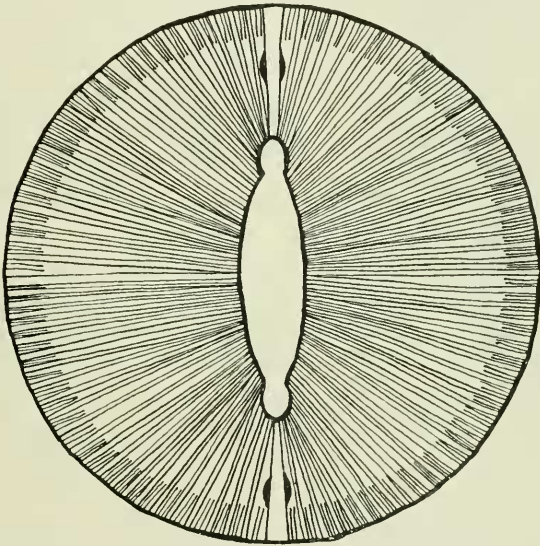


Diagram of a transverse section of *Phymactis clematis*, showing numerous perfect mesenteries.

families as links between the Actiniidae and Halcampidae, from near which they presumably arose. The three families might be compared with, for instance, the Diadumenidae, Metridiidae, and Sagartiidae of Part I—in which we have the same three grades of mesentery development, but acontia and cinclides and mesogloal sphincter in all. In our new trio there is a common absence of acontia and mesogloal sphincters and also of vesicles—as to cinclides it is hardly safe to say anything.

It has been so generally recognized that smooth-bodied and verrucose forms, and forms with and without acrorhagi cannot be separated into different families, that it seems hardly necessary to discuss this here.

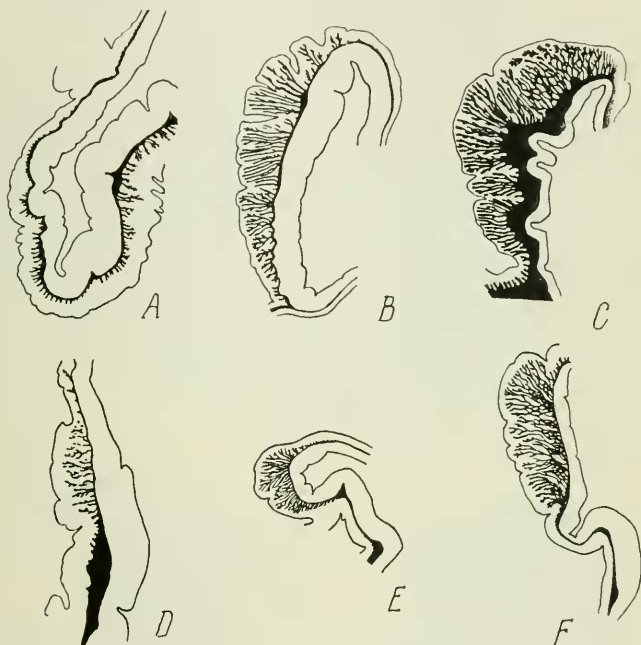
Secondly, there is the question of a separate Boloceridae. Such a family has been in use by some authors, and originally I felt a need for it (see 1918 A, p. 19), but further work has changed that feeling. It hardly seems that the deciduous tentacles are a character giving the *Boloceras* any right to separation, and otherwise they are exactly Actiniidae. This is especially the case since *Boloceroides* and *Bunodeopsis* have also the deciduous tentacles, and neither of them could be included in a Boloceridae in any case. One has to think of the cases as convergences. Even if *Bolocera* and *Bunodeopsis* should be further stages, along different lines, from a *Boloceroides*-like ancestor, this is no reason for classing the three together.

Thirdly, the Bunodidae. It seems a pity to have to attack an old-established family like this, but at the same time there seems to be no valid way whatever of separating it from the Actiniidae (in the revised sense), with which it is continuous.

Originally the Bunodidae relied for separation upon their verrucae and their strong circumscribed sphincters. The verrucal character was swept away by *Epiactis* and *Iso-tealia*, which are without it. We must now tackle the sphincter. In the first place the sphincter in *Bunodactis* (*Bunodes*) itself is variable, and often not a strong one. In the type-species, *B. gemmacea*, it may be half diffuse in some cases (I have sections of a very typical specimen showing this—see Text-fig. 11, D), and poorly developed. It is in *Tealia* and *Epiactis* (Text-fig. 12, A, B, C) that the really strong sphincters are found, and even there the size varies with species and individual. Further (this will be dealt with again under *Bunodactis* in Part III), there are apparently no criteria by which *Bunodactis* can be separated from *Anthopleura* and *Actinioides*, even generically—the three run right into each other and really form one large genus

varying as to sphincter from weak and diffuse to fairly strong and circumscribed—with too many grades to draw a line anywhere (a few are illustrated in Text-figs. 11 (D, F) and 12 (D, E)). And *Actinioides* is one of the genera hitherto

TEXT-FIG. 11.



Vertical sections of the sphincters of some Actiniidae, all drawn to same scale; showing various grades. A, *Condylactis* (here the sphincter is absent or practically so, what is shown being simply the upper part of the ordinary endodermal circular muscle). B, *Actinia equina*; C, *Bolocera tuediae*; D, *Bunodactis gemmacea*; E, *Anemonia sulcata*; F, *Bunodactis alfordi*. B and C are typical diffuse sphincters. D, E, and F are more of the circumscribed-diffuse grade. In all of them mesogloea is black, ectoderm and endoderm white.

classified as Actiniid. Proceeding still further towards the typical Actiniidae, if a comparative study of, for instance, *Bunodactis* (*Anthopleura*) *alfordi*, a *Condylactis*, and *Anemonia sulcata* be made, there is too much

similarity between them for any separation greater than generic to affect them.

In *B. alfordi* and *A. sulcata* there is a definite base, there are acrorhagi, long tentacles, lax habit of body only able to retract with great difficulty, similar habitat, weak to moderate circumscribed or circumscribed-diffuse sphincter (Text-fig. 11, E, F) (sometimes more diffuse in *sulcata*), numerous perfect mesenteries with fairly strong retractors, gonads on most of the older mesenteries, and the longitudinal musculature of the tentacles ectodermal. The chief difference is that *B. alfordi* has rows of verrucae which *A. sulcata* has not, and of course lesser species-differences. But obviously the relation is too close for the two to be included in different families, which has been done hitherto.

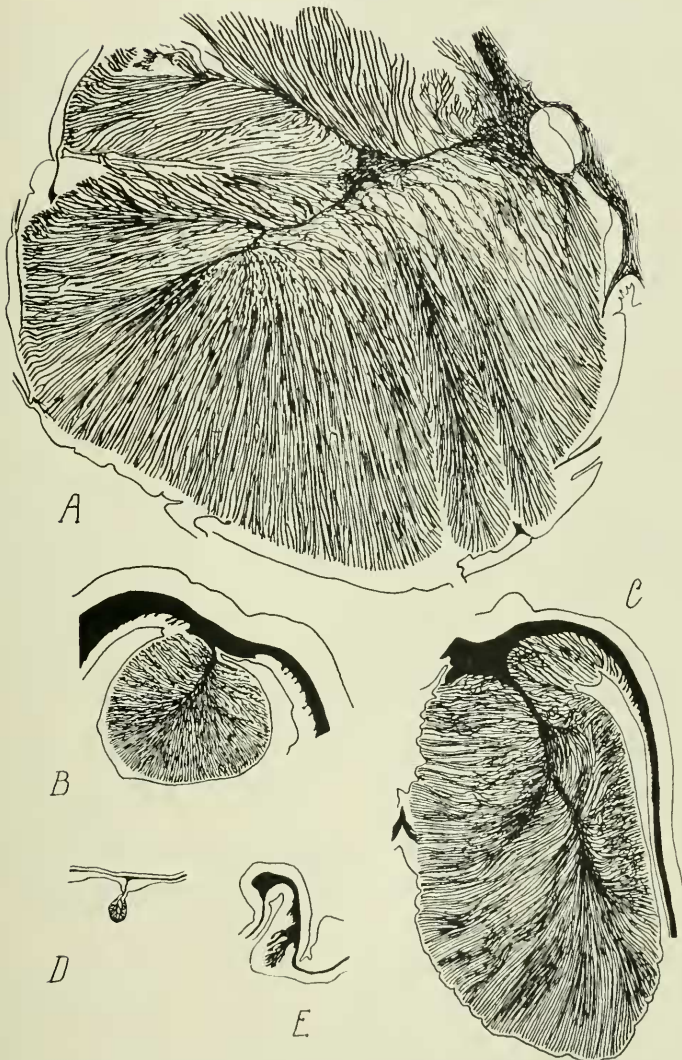
In *B. alfordi* and a *Condylactis* of which I have specimens, there is a definite base, there are verrucae, good tentacles, lax habit, numerous perfect mesenteries with fairly strong retractors, gonads on most of the older or all the mesenteries and ectodermal tentacular muscle. Here the main differences are lack of acrorhagi and a sphincter in the *Condylactis*. Between the points here given the similarity of the three genera should be clear. It is not always easy to distinguish them from each other if dealing with preserved material.

These things being so, where is the line to be drawn between Actiniidae and Bunodidae? Given a series of forms—such as *Anemonia*, *Condylactis*, *Bunodactis* (incl. *Actinio-* *ides* and *Anthopleura*), *Tealia*—where is the division?

Condylactis gives us verrucae but no acrorhagi and little or no sphincter; *Anemonia* has the acrorhagi but no verrucae, and a weakish circumscribed or diffuse sphincter; *B. alfordi* has both verrucae and acrorhagi and a moderate sphincter, \pm circumscribed (its relations showing other grades); and *Tealia* has verrucae (and rarely acrorhagi) and strong circumscribed sphincter.

The conclusion seems to be, clearly, that Bunodidae must be abandoned altogether. It should be noted that this does not impair the homogeneity of the Actiniidae, except as regards

TEXT-FIG. 12.



Further sphincters of Actiniidae for comparison with those in Text-fig. 11. All are to same scale as Text-fig. 11, and treated in the same way, but here we have various grades of circumscribed sphincter. The difference in size between A and B, for instance, is not due to a corresponding difference in size of the individuals from which they were taken. A, *Epiactis* sp.; B, *Tealia crassicornis*; C, *Epiactis novozealandica*; D, *Bunodactis* sp.; E, *Bunodactis balli*.

grade of sphincter; and that, it is evident, is bound to vary within the limits of some families.

A series of sphincters is illustrated in Text-figs. 11 and 12, all of them being taken from Actiniidae in the new sense. A more evenly graded set could, I think, be made, but I have not material for it. But this one brings out the facts that I have wished to emphasize fairly well.

§ K. The Forms with Vesicles.

The anemones provided with vesicles should (see p. 500) be kept apart from those without them, but among themselves there are two kinds at least.

Taking the vesicled genera together, one can list nine clearly-distinguished ones—*Alicia*, *Phyllodiscus*, *Thaumactis*, *Bunodeopsis*, *Phyllactis*, *Phymactis*, *Cradactis*, *Cystiactis*, and *Lebrunia*.

There have been families in existence to cover these forms (*Aliciidae*, *Phyllactidae*, *Dendromeliidae*, *Thaumactidae*), but the definitions have been based chiefly on the form and situation of the vesicles, and this seems as unnatural as it used to be to separate *Hormathia*, *Chitonactis*, *Chitonanthus*, and *Chondractinia* on account of variation in ridges and tubercles; and it has not been a very intelligible arrangement. So long as the vesicles are present, that is the family-character; their form and situation are more questions of generic distinction. From this point of view the families fall to the ground. The *Dendromeliidae* lapses in any case; it was formed to cover *Lebrunia* and *Ophiodiscus*. *Ophiodiscus* seems to be a typical *Paraetid* (see Part I, p. 560), and in the present state of our knowledge it seems very doubtful whether, although it is a distinct enough genus, there is anything to keep *Lebrunia* out of the *Phyllactidae*. The genus *Thaumactis* does not seem worthy, as we know it, to have a family to itself either. The other two families (*Aliciidae* and *Phyllactidae*) must be retained, but revised in the light of mesenterial arrangement, &c.

(a) *Alicia* and *Phyllodiscus* are delicate creatures with vesicled scapus and naked capitulum, or with the vesicles

at or at and above the scapo-capitular junction. There is little or no sphincter, and only six pairs of mesenteries are perfect. For these the name Aliciidae should be kept, and for these only.

(b) The other genera are provided, usually, with numerous perfect mesenteries, have various arrangements of vesicles, may be less delicate, and have sometimes circumscribed sphincters. Some of them have mesogloal longitudinal musculature in the tentacles. This collection has to be covered by the name Phyllactidae, and at that it had better be left for the moment. A fuller discussion of the family will fit better into Part III, where the generic definitions will be available for reference.

§ L. The Actiniidae and Vesicled Forms together.

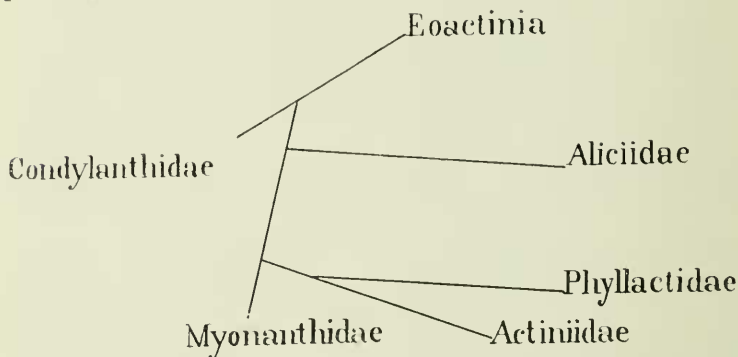
If the old Actiniidae and Bunodidae and Boloceridae (re-sorted into the new Actiniidae and Condylanthidae and Myonanthidae) and the Aliciidae and Phyllactidae be taken together, a mass of forms is presented exactly comparable to the set classified in Part I. It is worth while seeing whether they will work into a companion table like that on p. 481 in Part I. It is unfortunately necessary here to leave out cinclides, as there are not enough data about them. And of course absence of acontia and mesogloal sphincter go right through.

	No Vesicles.	Vesicles present.
Mesenteries divided into macro- and microcnemes. Number of macrocnemes six pairs.	Condylanthidae. Condylanthus. 7	No known representatives.
Mesenteries NOT divided into macro- and microcnemes. Number of perfect mesenteries six pairs.	Myonanthidae. Myonanthus. Macrodaactyla. Boloceroides. Nevadne. 7	Aliciidae. Alicia. Phyllodiscus. 8
Mesenteries NOT divided into macro- and microcnemes. Numerous perfect mesenteries, or at least more than six pairs in normal individuals.	Actiniidae. Actinia. Bolocera. Anemonia. Leipsiceras. Gyrostoma. Ixalactis. Condylactis. Pseudophellia. Bunodactis. Boloceroopsis. Tealia. Glyphostylum. Epiactis. Paranthoopsis. Isotealia. Dolleinia. 6	Phyllactidae. Phyllactis. Lebrunia. Phymactis. Thaumactis. Cradactis. Bunodeopsis Cystiactis. 6

In this table the number in the corner of each square is the number of characters which the members of the family in that square have in common.

Here the same characters as before go down the side of the table, but there are fewer to go above. And even without using the full number of combinations possible there is an empty square, no forms being yet described to fill it. Perhaps some will turn up, or perhaps it indicates that vesicles are structures not developed at stages of mesenterial evolution such as that represented by the Condylanthidae.

The diagram representing evolution in this group, as far as one may understand it, and for comparison with that given on p. 504 in Part I, would be as below. More will be said about it in the evolutionary section of the paper. An ancestral Eoactinia corresponding to the Eosagartia on the other line, may be imagined—a good deal like a Halcam-poides.



This diagram shows the Aliciidae and Phyllactidae as parallels, and involves the assumption that they arose independently from the main line, as some of them at any rate may probably enough have done. If they had a common origin among the pre-Actiniids, and the Phyllactids changed their mesenterial arrangement afterwards, or if some Phyllactids arose from early Actiniid forms and others from Aliciid forms, that would modify the diagram, but it is all speculation. Further details about it will be found under Phyllactidae in Part III.

§ M. The Minyadidae.

Probably unrelated forms have been placed here. There is little evidence of their relationship to each other, and there are few data altogether. It may later be found that there is no need for a Minyadidae, and that the contained forms may be allocated to different families as floating members. One form at least, *Nautactis olivacea*, Les., seems to be some sort of Stichodactyline. At the moment only *Stichophora torpedo*, Bell, can be defined, so far as I am aware, and that not fully; but for this form there seems to be justification for a family Minyadidae, even if it is not very clear, based on the definitely float-like character of the base taken with other things. At the present time it seems inopportune to say much about it, with the provision that so far there is no evidence of its ability to sustain higher than family rank, and it seems to fit in near the Actiniidae. If further details come to light—if, for instance, *S. torpedo* should have no ciliated tracts on its filaments—the position of the family will need reconsideration.

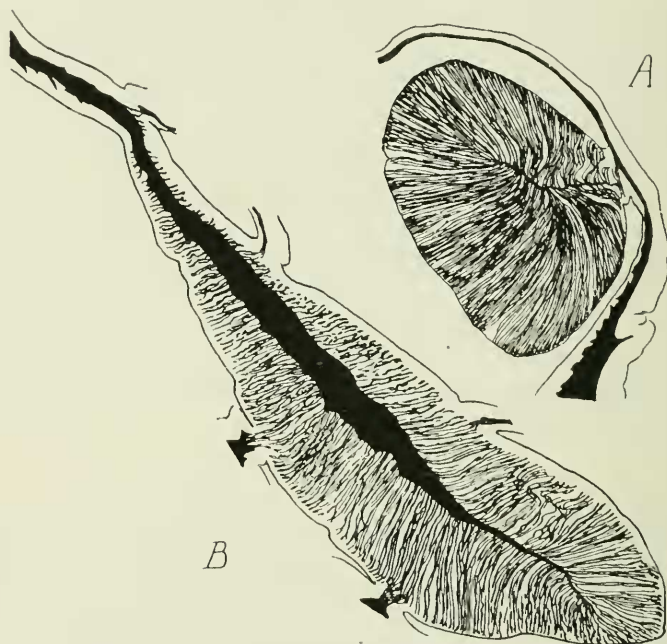
§ N. The Stichodactylines.

Here I have no suggestions to offer (save that already made about the Corallimorphidae and Discosomidae), but am prepared to accept fully the families defined by Carlgren in his 'Ostafrikanische Aktinien', 1900, and (Aurelianidae) in a smaller paper on Stichodactylines, also in 1900. These families seem to be excellently based and to represent relationships very naturally. They are the Stoichactidae, Thalassianthidae, Actinodendridae, Phymanthidae, Aurelianidae, Heteranthidae, and Homostichanthidae. They entirely supersede other arrangements, including Duerden's division of the group into Homodactylinae and Heterodactylinae; they will be defined in Part III.

There are a few points worth noting about the Stichodactylines in general, excluding always the Corallimorphidae and Discosomidae (this latter in the sense taken by Carlgren,

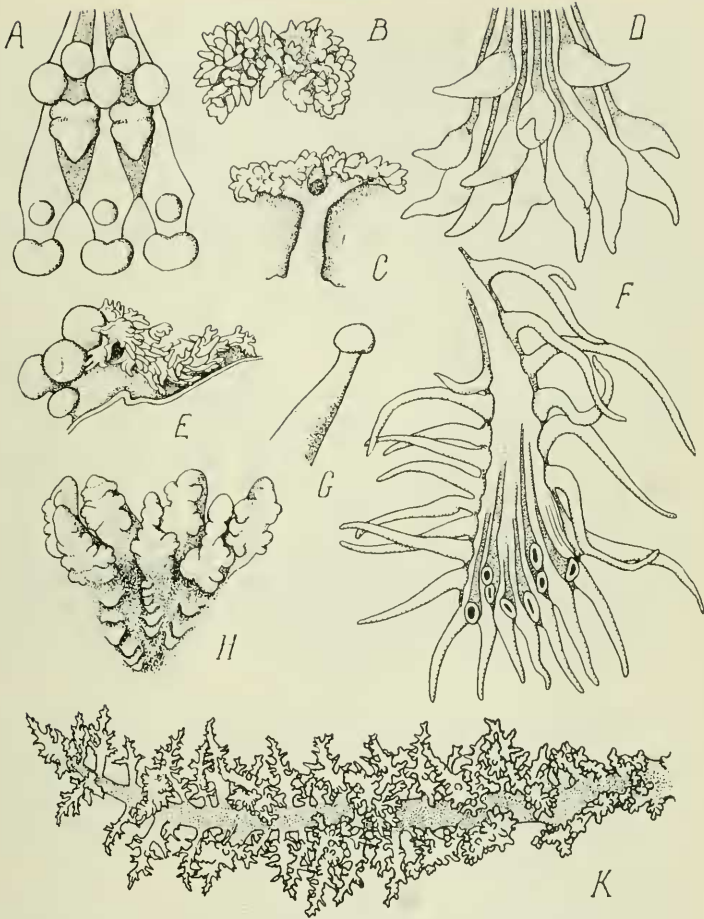
1900). In their main structural features they form a homogeneous group. In all of them (with rare exceptional individuals) there is more than one tentacle situated over at least some of the endocoels, and often over all the endocoels and even exocoels as well. The contrast between a Stichodactyline

TEXT-FIG. 13.



Vertical sections of two sphincters of Stichodactyline. A, *Actinoporus*; B, *Aureliania*.

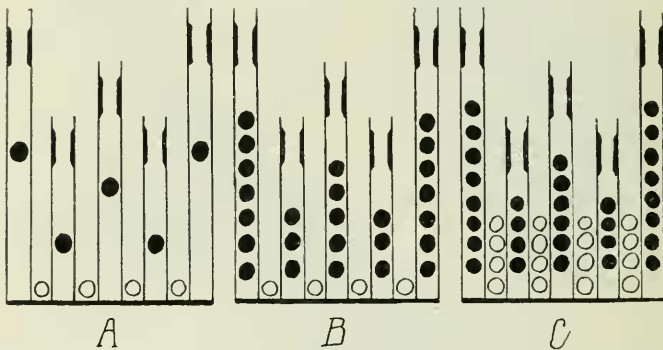
like *Cryptodendron* and an ordinary form (as regards tentacles) like *Phyllodiscus* is brought out in Text-fig. 2. A shows a vertical section of a whole specimen of the latter, and passes through one tentacle on each side of the mouth. B is a vertical section through a corner of the oral disc and body-wall of the former, and shows many short tentacles cut through in the same section—they do not all belong to the same mesenterial space, but they have not by any means one space to



Arrangement and form of tentacles. A, *Aureliania*, sector of disc, with various sorts of tentacles, and two to each exocoel and endocoel. B (surface view) and C (side view), of a dendritic tentacle of *Actinotryx*. In C the stem is embedded in the mesogloea of the disc. D is a sector of the disc of an Actiniine form with plain tentacles, one to each endocoel and exocoel. E, a radial group of dendritic tentacles and nematospheres from *Thalassianthus*. All this belongs to one endocoel. F, sector of disc of *Antheopsis* for contrast with D, showing some of the tentacles in endocoelic radial rows; here some of the tentacles have been cut off for the sake of clearness. G, knobbed tentacle of *Corallimorphus*. H, sector of disc of *Phymanthus*, showing marginal pinnate tentacles in alternating cycles and small disc-tentacles in radiating rows. The pinnate character is not very clear, as the specimen was distorted. K, arm or disc-lobe of *Megalactis*, bearing tentacles. (After Saville-Kent. See acknowledgement on p. 496.) In A, D, F, exocoels are white, endocoels shaded.

each. The contrast is differently brought out in Text-fig. 14, D and F, which represent two sectors of the oral disc of two forms. One of these (D) has the ordinary arrangement of tentacles in alternating cycles, one to each mesenterial space; the other (F) is from an *Antheopsis*, and shows two of the long radial rows situated over endocoels (which are shaded) and also the arrangement of the marginal tentacles, one or two to each endocoel, one to each exocoel (exocoels are not shaded).

TEXT-FIG. 15.



Diagrams of three types of tentacular arrangement. In each diagram three cycles of mesenteries are shown, with their retractor muscles as black thickening; endocoelic tentacles black, exocoelic white. In A there are cycles of tentacles, one tentacle only to each exocoel and endocoel. In B there are radial rows on the endocoels, but only one tentacle per exocoel (e. g. *Stoichactidae*). In C the exocoels as well as the endocoels have more than one tentacle (e. g. *Homostichanthidae*).

Stichodactylines have a definite base (occasionally reduced and half like a physa). Cinclides are recorded in at least one case (see p. 501). There is a complete absence of acontia and mesogloal sphincters, and almost complete absence of vesicles (there is one case of somewhat vesicular verrucae). The musculature is always reasonably well developed, at least in the mesenteries. There is either no approach to a division of the mesenteries into macro- and microenemes, or if there is, there are at least twelve pairs of the macroenemes; in the first case there are usually numerous perfect mesenteries.

Fundamental differences affect chiefly form and arrangement of tentacles and strength of musculature, and details about this will be found in Part III. Text-figs. 14 and 19 show some of the variation in tentacle-form to be found among Stichodactylines and skeletonless corals; Text-figs. 14 and 15 show some of the modes of arrangement; and Text-figs. 4 and 13 give details of musculature.

Taking them all in all it may be said that the Stichodactylines are the nearest analogue among anemones to the composites among plants or the birds among vertebrates. A good deal of fundamental structure is fixed, and variation more affects details or additional features. They may be looked upon as Endomyaria (see below) with, above all, tentacular specializations, often of a frilly nature.

§ O.

So far, taking this paper and Part I together, it has been sought to establish the thirty-two families listed below. It remains to discuss main subdivisions of the Anthozoa and arrangement of families within groups of higher rank.

Corallimorphidae.	Actiniidae.	Diadumenidae.
Discosomidae.	Aliciidae.	Phelliidae.
Gonactiniidae.	Phyllactidae.	Flosmarinidae.
Ptychodactidae.	Minyadidae.	Marsupiferidae.
Halcampidae.	Aurelianidae.	Metridiidae.
Ilyanthidae.	Stoichactidae.	Chondractiniidae.
Halcuriidae.	Homostichanthidae.	Actinoscyphiidae.
Actinernidae.	Actinodendridae.	Sagartiidae.
Condylanthidae.	Heteranthidae.	Choriactidae.
Myonanthidae.	Phymanthidae.	Paractidae.
Andresiidae.	Thalassianthidae.	

§ P. The Groups larger than families, and the Arrangement of the families within these Groups.

At this point discussion becomes more difficult and more dependent upon individual opinion. It may be simplest to start with the class Anthozoa and work downwards. Neither nomenclature nor main subdivisions are my special concern here, but probably no one will object to one of the following alternatives, whatever names be preferred.

Bourne's division is

- Sub-class 1. OCTACTINIARIA.
- Sub-class 2. CERANTIPATHARIA.
- Sub-class 3. ZOANTHACTINIARIA.

Or one could use

- Sub-class 1. OCTACTINIARIA.
- Sub-class 2. CERANTHARIA.
- Sub-class 3. ANTIPATHARIA.
- Sub-class 4. ZOANTHACTINIARIA.

Either of these is a good arrangement, probably, leaving aside the vexed question of Tetracorallia—it has recently been suggested that these may have something to do with the Endocoelactid type of structure.

The next step is the subdivision of the Zoanthactiniaria. Few will object to having the Zoanthids as a separate set among them, and although Edwardsiids are sometimes included with ordinary anemones, Bourne has recently shown that they must rank as a distinct group equal to that containing the Zoanthids. So the Zoanthactiniaria may be divided into three or four, with a number of common tendencies (see p. 551).

Bourne subdivides thus :

- Order 1. ZOANTHINARIA.
- Order 2. EDWARDSIARIA.
- Order 3. DODECACTINIARIA.

His order Dodecactiniaria includes the sub-orders Actiniaria and Madreporaria. Carlgren, however, divides slightly differently.

- Order 1. ZOANTHARIA.
- Order 2. ACTINIARIA.
- Order 3. MADREPORARIA.

To this, now, *Edwardsiaria* would have to be added. In this paper Bourne's division will be used. It is when we come to the subdivision of the sub-order Actiniaria that the main divergence of opinion begins.

Carlgren divides into

- Tribe 1. PROTANTHEAE.
- Tribe 2. NYNANTHEAE.

Another division in use is

- Tribe 1. ACTINIINAE.
- Tribe 2. STICHODACTYLINAE.

In the following paragraphs I shall indicate the lines of grouping which I wish to suggest, giving an outline only. Further reasons, filling in this outline, will be found in various parts of the paper, especially under the foregoing sections dealing with sets of forms individually, and in the later evolutionary discussions.

Much has been said about Carlgren's division into Protantheae and Nynantheae, and it has been rejected by some workers, at any rate, in the sense in which Carlgren uses it. It is based mainly upon the presence or absence of ectodermal muscle and a nerve-layer in the ectoderm of body-wall and actinopharynx; and this, as has been suggested before, is probably a universal ancestral character surviving in more or less primitive forms and, otherwise, in sporadic cases. I cannot accept it as a good basis of distinction in itself, although it helps to show relationships, in some cases, when taken with other things. In this attitude I believe I am in agreement with Haddon (1898, p. 411), Duerden (1900, p. 137, and 1902), McMurrich (1904) and Bourne. At the same time I accept decidedly Carlgren's Protantheae, but in a different and much more restricted sense. I have tried to show that Carlgren's Protostichodactylines (a sub-tribe of his Protantheae) (and also the Discosomidae) are corals (see p. 510), and this restricts his Protantheae to Gonaactiniidae, Ptychodactidae, and the

Endocœlactids. As mentioned on p. 523, the Endocœlactids seem to be definitely post-Halcampid and Nynanthean, and will here be treated as such. This leaves us with the Gonaetiniidae and Ptychodactidae (see pp. 508, &c.); and I feel that these represent two different side-lines of evolution, not necessarily very close together even though both have some primitive features, and that in this case it is safer to give each a group, the two equal in rank. I therefore propose to limit the Protantheae to the Gonaetiniidae (in the sense taken on p. 505 and exclusive of *Boloceroïdes*), and to erect a group Ptychodacteae for the Ptychodactids, equal in rank to Protantheae and Nynantheae. The Nynantheae I accept as the main tribe, provided it include *Boloceroïdes* (see p. 506) and the Endocœlactids (see p. 522), and exclude the Edwardsiids and 'soft' corals (see p. 510); and provided that not only it, but also the other tribes, be re-defined on the sum of their main characters and not on the presence or absence of ectodermal muscle in the body-wall, simply.

My suggestion for subdividing Actiniaria is therefore this one:

Tribe 1. PROTANTHAEAE (including Gonaetiniidae only, and not *Boloceroïdes*).

Tribe 2. PTYCHODACTEAE (including Ptychodactidae).

Tribe 3. NYNANTHAEAE (including *Boloceroïdes* and Endocœlactids, and majority-forms, excluding Edwardsiids and skeletonless corals).

With regard to the other subdivision of Actiniaria into Actiniinae and Stichodactylinae—I used this, provisionally only, in Part I, but am letting it lapse here in favour of the above scheme. One feels that these groups have been useful as a half-way house, but that in the light of developing knowledge of the group, it is now possible to go farther. The 'Actiniine' condition is found in all Nynantheae save one section; it prevails also in Protantheae, Ptychodacteae, and most corals. 'Stichodactylinism' occurs in Ceriantharia and a few corals, and in one set of Nynantheae. There are, however, among Nynantheae, four quite distinct sets, seemingly repre-

senting four lines of evolution; and the 'Stichodactyline' form a compact group within one of these four sets. These four groups can be defined by the sums of their main characters, and clearly the Actiniine-Stichodactyline contrast must be used simply in connexion with a subordinate division of that one of the four groups in which it occurs—if it be used at all. This is only making it one degree more subordinate than Carlgren does in his scheme. It is evident that as primary subdivisions of Actinaria the two groups are no longer adequate—they must be reduced in rank, at least, from tribes to less than sub-tribes.

Carlgren's scheme is :

Tribe NYNANTHEAE.

Sub-tribe 1. Actiniinea.

a. Athenaria.

b. Thenaria.

Sub-tribe 2. Stichodactylinae.

The grouping I wish to suggest, as expressive of the above-mentioned four main lines of Nynanthean evolution, is :

Tribe NYNANTHEAE.

Sub-tribe 1. Athenaria.

Sub-tribe 2. Endocoelactaria.

Sub-tribe 3. Mesomyaria.

Sub-tribe 4. Endomyaria.

a. Actiniinae.

b. Stichodactylinae.

I have put in the Actiniinae and Stichodactylinae where they must come, if used, in this scheme—as subordinate to Endomyaria.

The Athenaria of this plan is Carlgren's Athenaria without the Edwardsiids. I fully agree that it is a good group—but it represents a line of evolution within Nynantheae, all of which are derivatives of a Halcampa-like stage, and needs no subordination to anything else. Nor is there any need for a contrasting group Thenaria; the other three tribes are mostly 'Thenaria', but they represent three evolutionary lines and are best kept independent (see p. 560 et seq.).

The *Endocoelactaria* form a decided small line apart, and with very distinct characters (see p. 522), and it seems inevitable to give them a group to themselves. Since they seem clearly post-Halcampid, this group must come under *Nynantheae*, not outside it; and is distinct enough from other *Nynantheae* to require no further subordination.

This leaves the *Mesomyaria* and *Endomyaria*, or main mass of forms. It has been part of the purpose of this paper to show that this main mass does fall into two chief sets, following two great lines of tendency, and these two lines I propose to embody in the two sub-tribes named. The *Mesomyaria* contains the forms classified in Part I, the creatures with acontia and mesogloecal sphincters and so on; the *Endomyaria* contains those with no mesogloecal (and typically an endodermal) sphincter, no acontia, and often with vesicles, frills, &c.—for more detail of *Endomyarian* and *Mesomyarian* tendencies see pp. 560 et seq. The *Endomyaria* contains the whole of the old *Stichodactylinae* (save soft corals) and part of the *Actininae*, and if those names be still used it should be only as subdivisions of this group.

For most of the matter supporting the various suggestions made in this section, reference should be made to the sections on evolution and on special sets of forms, and other parts, both in this paper and in Part I.

It now remains to allocate the families listed on p. 537 to their respective groups.

1. PROTANTHEAE. Gonaetiniidae.
2. PTYCHODACTEAE. Ptychodactidae.
3. NYNANTHEAE.
 - A. ATHENARIA. Halcampidae, Ilyanthidae.
 - B. ENDOCOELACTARIA. Halcouriidae, Actinernidae.
 - C. MESOMYARIA. Diadumenidae, Phelliidae, Flosmarinidae, Marsupiferidae, Metridiidae, Chondractiniidae, Actinoscyphiidae, Sagartiidae, Choriaetidae, Paraetidae.
 - D. ENDOMYARIA. Condylanthidae, Myonanthidae, Andresiidae, Actiniidae, Aliciidae, Phyllactidae, Minyadidae, Phymanthidae, Heteranthidae, Stoichaetidae, Actinodendridae, Thalassianthidae, Homostichanthidae, Aurelianidae. Discosomidae and Corallimorphidae go to Madreporaria.

§ Q. Summation of Characters.

In case it should be felt that the foregoing sections are too much of an outline and have too much connexion with evolutionary speculation, it seems advisable to point out that the conclusions have the backing of the sum-of-the-characters principle. The following lists will show that the groups suggested have a solid number of characters binding them together. Only main features are included. In connexion with some of the details given under the larger groups, Text-fig. 16 will be found useful. I will take families first, then larger groups.

FAMILIES.

GONACTINIIDÆ. Genera: *Gonactinia*, *Protanthea*.
Common characters, 11.

1. Definite base. 2. No basilar muscles. 3. Ectodermal muscle in body-wall and actinopharynx. 4. Spirocysts in ectoderm of body-wall (and actinopharynx?). 5. No developed sphincter. 6. Tentacular longitudinal muscle ectodermal. 7. No true siphonoglyphes. 8. Only the eight protocnemes perfect. 9. Mesenterial musculature weak, not forming true retractors. 10. Filaments without ciliated tracts. 11. No acontia.

PTYCHODACTIDÆ. Genera: *Ptychodactis*, *Dactylanthus*. Common characters, 12.

1. Definite base. 2. No basilar muscles. 3. Ectodermal muscle in body-wall and actinopharynx. 4. Spirocysts in ectoderm of body-wall (and actinopharynx?). 5. No developed sphincter. 6. Tentacular longitudinal muscle ectodermal. 7. At least six, usually twelve or more, pairs of perfect mesenteries. 8. Weak mesenterial musculature, hardly forming retractors. 9. Filaments with no ciliated tracts. 10. Filaments of imperfect mesenteries with curious half-funnels at upper termination. 11. Mesenteries with the free edge (or its analogue) occupied by filament above, gonad below, if present. 12. No acontia.

CORALLIMORPHIDÆ. Genera: *Corallimorphus*, *Corynactis*, *Isocorallion*. Common characters, 16.

1. No horny or limy skeleton. 2. Definite base. 3. No basilar muscles. 4. Ectodermal muscle in body-wall, at least sometimes, perhaps always. 5. Large sting-cells typically present in some part

of body. 6. No developed sphincter. 7. Tentacular longitudinal muscle ectodermal. 8. Tentacles not branched, but knobbed. 9. More than one tentacle on at least each of the strongest endocoels. 10. Not more than one tentacle per exocoel. 11. No true siphonoglyphes.¹ 12. No division of mesenteries into macro- and microcnemes. 13. Usually numerous perfect mesenteries. 14. Feeble mesenterial musculature. 15. Filaments with no ciliated tracts. 16. No acontia.

DISCOSOMIDAE. Genera: *Discosoma*, *Paradiscosoma*, *Orinia*, *Actinotryx*, *Ricordea*, *Rhodactis*.
Common characters, 12.

1. No horny or limy skeleton. 2. Definite base. 3. No basilar muscles. 4. No developed sphincter. 5. Tentacular longitudinal muscle ectodermal, such as it is. 6. More than one tentacle on at least each of the stronger endocoels. 7. No true siphonoglyphes.¹ 8. No division of mesenteries into macro- and microcnemes. 9. Usually numerous perfect mesenteries. 10. Feeble mesenterial musculature, not forming true retractors. 11. Filaments without ciliated tracts. 12. No acontia.

N.B.—In this family the tentacles may be reduced or practically absent, and their form is variable; sometimes there is more than one, on exocoels as well as endocoels.

HALCAMPIDAE. Genera: *Halcampa*, *Halcampoides*, *Pentactinia*, *Scytophorus*. Common characters, 8.

1. No base (correlated with more or less vermiform shape). 2. No basilar muscles. 3. Sphincter absent or weak (if present may be mesogloecal or endodermal). 4. Tentacular longitudinal muscle ectodermal. 5. Mesenteries divided into macro- and microcnemes, or all macrocnemes. 6. Six pairs of macrocnemes the average (may be four or five to seven couples). 7. Few mesenteries and tentacles—up to forty or so. 8. No acontia.

ILYANTHIDAE. Genera: *Ilyanthus* (*mitchelli*), *Peachia*, *Eloactis*, *Haloelava*, *Harenactis*. Common characters, 8.

1. No base. 2. No basilar muscles. 3. No developed sphincter. 4. Tentacular longitudinal muscle ectodermal. 5. Mesenteries all

¹ With regard to this statement, see definition in Part III. covering *Corallimorphidae* and *Discosomidae*.

macrocnemes (in one case macrocnemes and some of an intermediate sort). 6. Never fewer than ten pairs of mesenteries, mesenteries all perfect (one exception). 7. Few mesenteries and tentacles--up to forty or so. 8. No acontia.

HALCURIIDAE. Genera: *Halcurias*, *Carlgrenia*. Common characters, 8.

1. Definite base. 2. Spirocysts in ectoderm of body-wall nearly always. 3. No sphincter. 4. Tentacular longitudinal muscle ectodermal. 5. Only one siphonoglyphe. 6. After the first six pairs, mesenteries develop as directives and in endocoels. 7. There is a fairly sharp division between the first six or ten pairs and the rest, the former being macrocnemes and the latter more or less microcnemes; retractors of macrocnemes circumscribed. 8. No acontia.

ACTINERNIDAE. Genera: *Actinernus*, *Isactinernus*, *Synactinernus*, *Synhalcurias*. Common characters, 10.

1. Definite base. 2. Spirocysts in ectoderm of body-wall. 3. No sphincter. 4. Tentacular longitudinal muscle ectodermal (or with mesogloal tendency in part). 5. Two siphonoglyphes. 6. After the first six pairs mesenteries develop as directives and in endocoels. 7. No division of mesenteries into macro- and microcnemes. 8. Numerous perfect mesenteries. 9. Mesenterial musculature not strong. 10. No acontia.

CONDYLANTHIDAE. Genus: *Condylanthus*. Main characters, 7.

1. Definite base. 2. No vesicles. 3. No sphincter. 4. Tentacular longitudinal muscle ectodermal. 5. Mesenteries divided into macro- and microcnemes. 6. Macrocnemes six pairs. 7. No acontia.

MYONANTHIDAE. Genera: *Myonanthus*, *Macrodaetyla*, *Boloceroides*, *Nevadne*. Common characters, 7.

1. Definite base. 2. No vesicles. 3. No mesogloal sphincter (sphincter endodermal or absent). 4. Tentacular longitudinal muscle ectodermal. 5. Mesenteries not divided into macro- and microcnemes. 6. Perfect mesenteries six pairs. 7. No acontia.

ANDRESIIDAE. Genus: *Andresia*. (One species only, see p. 518.) Main characters, 7.

1. No base (correlated with very extensile body). 2. No vesicles. 3. Small circumscribed endodermal sphincter. 4. Tentacular longi-

tudinal muscle ectodermal. 5. Mesenteries not divided into macro- and microcnemes. 6. All mesenteries perfect. 7. No acontia.

It has long tentacles in graded cycles.

ACTINIIDAE. Genera: *Actinia*, *Anemonia*, *Gyrostoma*, *Condylaetis*, *Parantheopsis*, *Bunodactis*, *Tealia*, *Epiactis*, *Isotealia*, *Bolocera*, *Leipsiceras*, *Boloceropsis*, *Dofleinia*, *Glyphostylum*, *Pseudophellia*, *Ixaetis*.
Common characters, 6.

1. Definite base. 2. No vesicles. 3. No mesogloal sphincter (sphincter absent or endodermal). 4. Mesenteries not divided into macro- and microcnemes. 5. Numerous perfect mesenteries—at the least more than six pairs in adults. 6. No acontia.

This is one of the few families in which the longitudinal muscle of the tentacles is sometimes mesogloal.

ALICIIDAE. Genera: *Alicia*, *Phyllodiscus*. Common characters, 8.

1. Definite base. 2. Vesicles present. 3. Body-wall delicate, divided into scapus and capitulum, the vesicles occurring either on the scapus or at and above its junction with the capitulum. 4. No mesogloal sphincter, no developed sphincter at all. 5. Tentacular longitudinal muscle ectodermal. 6. Mesenteries not divided into macro- and microcnemes. 7. Six pairs of perfect mesenteries. 8. No acontia.

PHYLLACTIDAE. Genera: *Phyllactis*, *Cradaetis*, *Phymactis*, *Cystiaetis*, *Lebrunia*, *Bunodeopsis*, *Thaumaetis*. Common characters, 6.

1. Definite base. 2. Vesicles present. 3. No mesogloal sphincter (sphincter endodermal or absent). 4. Mesenteries not divided into macro- and microcnemes. 5. Numerous perfect mesenteries as a rule. 6. No acontia.

Here again tentacular longitudinal muscle may be ectodermal or mesogloal.

MINYADIDAE. Genus: *Stichophora*. Chief characters, 7.

1. Base a float. 2. No vesicles. 3. Sphincter endodermal. 4. One siphonoglyphe. 5. Mesenteries not divided into macro- and microcnemes. 6. Ten pairs of perfect mesenteries. 7. No acontia.

AURELIANIDAE. Genera: Aureliania, Actinoporus.

Common characters, 9.

1. Definite base. 2. Sphincter strong endodermal circumscribed. 3. Tentacles have the form of small vesicles, and may be lobed. 4. More than one tentacle to each main endocoel. 5. More than one tentacle to each main exocoel. 6. One siphonoglyphe. 7. All the mesenteries, or all the older ones, perfect. 8. Mesenteries either all with the grade of macrocnemes (and with unusually strong circumscribed retractors), or else more or less divided into macro- and microcnemes. 9. No acontia.

Here the disc and tentacle radial muscle may be ectodermal or mesogloal, and there are vesicular verrucae in one genus.

PHYMANTHIDAE. Genus: Phymanthus. Main characters, 10.

1. Definite base, sometimes reduced. 2. No vesicles. 3. No developed sphincter. 4. Disc and tentacle radial muscle ectodermal or with a mesogloal tendency. 5. Tentacles divided into marginal and discal, the former tentaculiform and usually pinnate, the latter more usually papilliform (rarely they are absent). 6. Marginal tentacles not more than one per exo- and endocoel. 7. Discal tentacles typically in radial rows—they may occur on exocoels as well as endocoels. 8. Mesenteries not properly divided into macro- and microcnemes as a rule, though coming very near it sometimes. 9. Numerous perfect mesenteries. 10. No acontia.

ACTINODENDRIDAE. Genera: Actinodendron, Megalactis, Actinostephanus. Common characters, 10.

1. Definite base. 2. No vesicles. 3. No developed sphincter. 4. Disc and tentacle radial muscle ectodermal. 5. Disc produced into permanent arm-like lobes. 6. Numerous tentacles per endocoel. 7. Numerous tentacles per exocoel. 8. Mesenteries not divided into macro- and microcnemes. 9. Numerous perfect mesenteries. 10. No acontia.

HOMOSTICHANTHIDAE. Genus: Homostichanthus. Main characters, 11.

1. Definite base. 2. No vesicles. 3. Sphincter endodermal, not strong. 4. Oral disc not formed into arm-like permanent lobes. 5. Tentacles short and papilla-like, simple. 6. Numerous tentacles per endocoel. 7. Numerous tentacles per exocoel. 8. Tentacular longitudinal muscle ectodermal. 9. Mesenteries not divided into

macro- and microcnemes. 10. Numerous perfect mesenteries. 11. No acontia.

THALASSIANTHIDAE. Genera: *Thalassianthus*, *Cryptodendron*, *Actineria*. Common characters, 10.

1. Definite base. 2. No vesicles. 3. Sphincter endodermal, not very strong, may be circumscribed. 4. Disc and tentacle radial muscle ectodermal. 5. Tentacles divided into dendrites and nematospheres. 6. Not more than one dendritic tentacle per exocoel, and no nematospheres. 7. Typically more than one dendrite, and nematospheres, on endocoels. 8. Mesenteries not divided into macro- and microcnemes. 9. Numerous mesenteries perfect. 10. No acontia.

STOICHIACTIDAE. Genera: *Stoichactis*, *Radianthus*, *Antheopsis*. Common characters, 11.

1. Definite base. 2. No vesicles. 3. Sphincter endodermal, strong or not very strong, may be circumscribed. 4. Tentacular longitudinal muscle ectodermal. 5. Oral disc not produced into permanent arm-like lobes. 6. Tentacles simple, all of one sort (but for sporadic cleft ones which are sometimes present). 7. Not more than one tentacle per exocoel. 8. More than one tentacle on at least each older endocoel, except in very rare cases; usually some or all of the endocoels have several or many. 9. Mesenteries not divided into macro- and microcnemes. 10. Numerous perfect mesenteries. 11. No acontia.

HETERANTHIDAE. Genus: *Heteranthus*. Chief characters, 9.

1. Definite base. 2. No vesicles. 3. Sphincter endodermal, not very strong, circumscribed. 4. Tentacles of two sorts, marginal and discal. 5. Oral disc not produced into permanent arm-like lobes. 6. Marginal tentacles short conical, disc-tentacles wart-like. 7. Mesenteries not divided into macro- and microcnemes. 8. Numerous perfect mesenteries. 9. No acontia.

The other ten families were listed and dealt with in Part I. It will be seen from an inspection of the above lists, that at the minimum each family has six common characters, and most have 7 to 11, a few even more. It must also be remembered that the lists are not exhaustive, and that most of them could be added to and even some of the characters subdivided. For instance, 'presence of ciliated tracts on the mesenterial

filaments', 'presence of basilar muscles', 'absence of ectodermal muscle in body-wall', 'presence of not more than one tentacle per exo- and endocoel', and so on, could be added where suitable; but the addition of all these where not strictly required for present purposes would be needlessly complicating—it is mentioned only to show that the lists could be expanded rather than otherwise.

I should like to repeat here a remark made in Part I, to the effect that the arrangement suggested cannot be validly criticized on the ground that in some cases there are only one or two differences between two given families. Provided that the differences are good ones, this is all right—if families be fused up on that principle it is soon found that the whole Actinaria will go into one or two collections, and classification breaks down altogether. The very fact that the families form enough of a series to have few differences sometimes, supports the idea that they represent relationships truly.

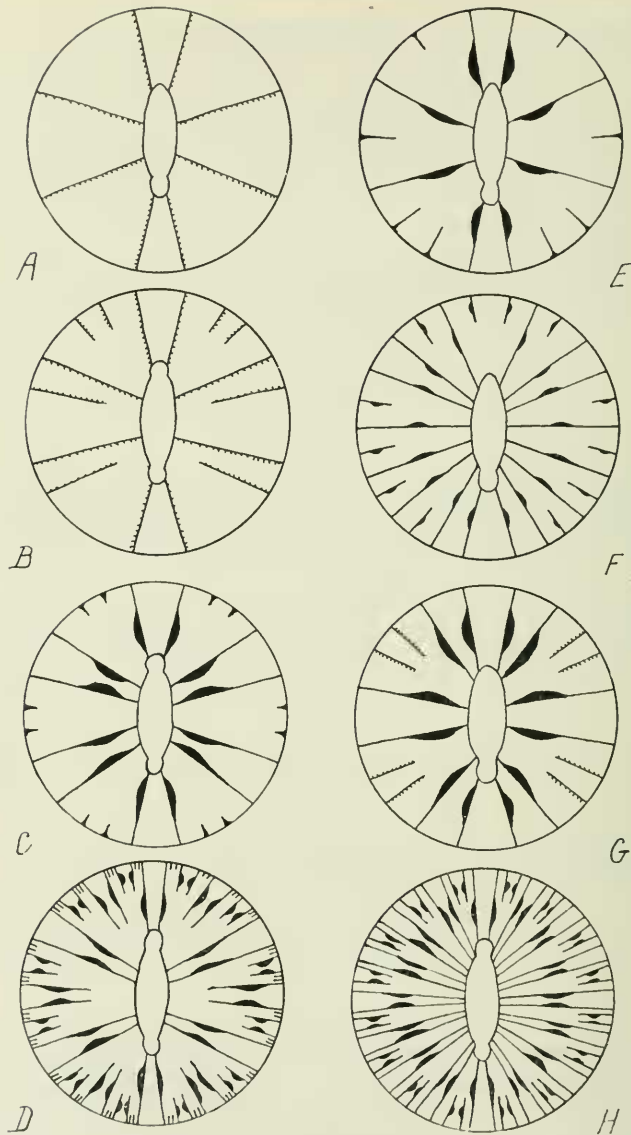
If sums-of-characters for groups of wider inclusion than families be now taken, the difficulty of course arises that they can be made less absolute, because in some cases there are one or two exceptions to almost everything among large series of anemones, and this is the same whatever classification be adopted. It must therefore suffice to make definitions of tendency rather than of exclusive fact, in some cases.

GROUPS LARGER THAN FAMILIES.

Here the wider groups will be taken first.

Class ANTHOZOA. Sub-classes included: Ceriantipatharia, Octactinaria, Zoanthactinaria.
Common characters or tendencies, 14.

Coelenterata with (i) no medusae, (ii) 'hydroid-generation' form, (iii) nematocysts, (iv) characteristic muscularity as compared with Hydrozoa, (v) bilateral symmetry typically, (vi) no primary cruciform symmetry like that of Scyphozoa, (vii) mesenteries, (viii) no septal funnels, (ix) no endodermal tentacles, (x) mesenterial filaments, (xi) endodermal gonads borne on the mesenteries, (xii) an actinopharynx, (xiii) no canal-system comparable to that of a Scyphozoan, (xiv) no specialized sense-organs in adults.



Diagrams of transverse sections showing various mesenterial formulae. A, supposed ancestor of Zoanthactinaria; B, *Gonactinia*; C, *Halcampa*; D, form with graded cycles of mesenteries but only six pairs perfect (e.g. *Myonanthidae*); E, an *Edwardsia*; F, *Parazoanthus*; G, *Carlgrenia*; H, form with graded cycles of mesenteries, and sixteen pairs perfect. Compare this with a further stage shown in Text-fig. 10.

Sub-class ZOANTHACTINIARIA. Orders included: Edwardsiaria, Zoanthinaria, Dodecactiniaria. Common characters or tendencies, 9.

1. Directive mesenteries typically present, two pairs the standard number. 2. The directive endocoels do not become subdivided in most forms, but it may occur. 3. There are always more than eight mesenteries, even if only eight strong ones, in adults. 4. The eight protoconemes do not typically get pushed out of the way in the manner typical of Ceriantharia. 5. In most cases the mesenteries form pairs, not couples. 6. There are never just eight pinnate tentacles; pinnate tentacles at all are rare, and occur in a few forms of obvious relationships. 7. There are no gular tentacles like those of Cerianthids. 8. There is no sheet of muscle in the body-wall ectoderm comparable in strength to that of Cerianthids. 9. There is no horny axis like that of Antipatharia.

Order DODECACTINIARIA. Sub-orders included: Madreporaria, Actiniaria. Common characters or tendencies, 6.

1. More than eight mesenteries, but there may be only eight perfect: but even so some imperfect ones pair with them: usually at least six pairs perfect. 2. After the first six couples, typically pairs in cycles are formed. 3. Both pairs of directives, if present, are perfect, not one pair macro- and the other micromesenteries as in Zoanthids. 4. The later mesenteries are not typically confined to two lateral regions of growth only, as in Zoanthids, though they may come in the directive endocoels. 5. Mesenteries not typically formed in unequal pairs, one perfect and macromesenteric and the other not, as in Zoanthids. 6. No canals in the body-wall save in the case of some skeleton-building forms.

Sub-order ACTINIARIA. Tribes included: Protantheae, Ptychodacteeae, Nynantheae. Common characters or tendencies, 6.

1. No horny or limy skeleton. 2. No colonies. 3. Sting-cells of Madreporarian type do not occur much. 4. Tendency to muscularity greater than in Madreporaria, but not found in the most primitive forms and some others. 5. Siphonoglyphes present in the majority, but not in certain primitive and other forms. 6. Save in the earlier forms, the mesenterial filaments have ciliated tracts.

Tribe PROTANTHAEAE. 1 family. See Gonactiniidae for characters.

Tribe **PTYCHODACTEAE**. 1 family. See *Ptychodaetidae* for characters.

Tribe **NYNANTHEAE**. Sub-tribes included: *Athenaria*, *Endocoelactaria*, *Mesomyaria*, *Endomyaria*. Common characters or tendencies, 7.

1. Ectodermal muscle in body-wall the exception and not the rule, occurring only in sporadically-distributed cases.
2. Spirocysts in body-wall ectoderm not the rule—only of regular occurrence in *Endocoelactids*.
3. Siphonoglyphs present save in odd cases.
4. Mesenterial filaments with ciliated tracts.
5. Pairs of perfect mesenteries present.
6. Mesenterial musculature does not very often exhibit so low a grade of development as in the *Gonaetimiidae*, *Ptychodaetidae*, and many *Madreporaria*, weakness being usually sporadic and secondary rather than universal and inherent.
7. A fundamental number for the arrangement of parts is six, but there are a good many deviations.

Sub-tribe **ATHENARIA**. 2 families. Common characters, 9.

1. No base (correlated with more or less vermiform shape).
2. No basilar muscles.
3. No vesicles.
4. Sphincters weak or absent, though if present they may be endodermal or mesogloal.
5. Not more than one tentacle per exo- and endocoel.
6. Tentacles and mesenteries few, up to forty or so.
7. Secondary mesenteries exocoelic.
8. Mesenteries divided into macro- and microenemes, or all macroenemes, with *Peachia* as an intermediate.
9. No acontia.

Sub-tribe **ENDOCOELACTARIA**. 2 families. Common characters, 9.

1. Definite base.
2. No genuine basilar muscles.
3. No vesicles.
4. Spirocysts nearly always in body-wall ectoderm.
5. Probably no ectodermal muscle in body-wall.
6. No sphincter.
7. Secondary mesenteries endocoelic and oriented as directives.
8. Not more than one tentacle per exo- and endocoel.
9. No acontia.

Sub-tribe **MESOMYARIA**. 10 families. Common characters or tendencies, 7.

1. Definite base with one or two exceptions.
2. Basilar muscles usually present.
3. No vesicles.
4. Acontia or a mesogloal sphincter, or both, present.
5. Not more than one tentacle per endo- and exocoel.
6. Secondary mesenteries exocoelic.
7. No acrorhagi or tentacular complications of an *Endomyarian* sort—often there are basal mesogloal swellings to the tentacles, and thick body-walls, however, and there are two cases of another sort of tentacular thickening.

Sub-tribe ENDOMYARIA. 14 families. Common characters or tendencies, 6.

1. Definite base save in one case (it may be somewhat reduced, or may form a float). 2. Basilar muscles usually present. 3. No mesogloal sphincters (sphincter endodermal if present). 4. No acontia. 5. Secondary mesenteries exocoelie. 6. There may be no external complications of the body or tentacles, but verrucae, aerorhagi, vesicles, and complex tentacles are characteristic of different members of the group, more than one of them sometimes occurring in the same form; but there are no tentacles with basal mesogloal swellings.

Here there is often more than one tentacle on an endocoel, and there may be a good many on each main endo- and exocoel; or, on the other hand, there may be not more than one to each.

The above lists show that even when one is dealing with larger groups it is generally possible to base them on a fair sum of characters or at least of tendencies. It should of course be remembered that each family has not only its own special family-features, as listed, in common, but also many of the group-characters behind the family. To take a single example, the Actiniidae have in common 6 Actiniid characters + 6 Endomyarian features + 7 Nynanthean characters + 6 Actinarian characters + 6 Dodeactinarian characters + 9 Zoanthactinarian + 14 Anthozoan, not to mention all their Coelenterate and Metazoan points. So that they have, back to Anthozoa, 54 common characters—the number has to be reduced of course by any characters which may occur in more than one of the lists involved, or which may be inapplicable to the particular case in point, but even then the number will be considerable.

5. EVOLUTIONARY SUGGESTIONS.

That the classification suggested here has a firm foundation in character-summation will be evident from the above lists and the definitions later on; but it allows a certain amount of latitude for alternative ideas of evolutionary history, with which it is necessarily a good deal mixed up, especially in cases of large groups, where one is almost bound to think partly

in terms of evolution. The view here taken of the evolution of the forms will now be further developed.

In Part I reasons were given for thinking of a *Halcampa*-like form as more primitive than such a creature as *Catadiomene* (though of course more advanced than *Gonaetinia*), and it was concluded that whatever the detail, the main direction of evolution would be in the direction *Halcampa*-form \longrightarrow *Catadiomene* and not the reverse, and that this would generally apply. Without going into it all again (see Part I, p. 487) it may be assumed that in dealing with such a group as the *Endomyaria*, some *Halcampoides*-like form is the end to start at, and *Tealia* or *Phymactis*, or some *Stichodactyline* the antithesis, for much the same sort of reason, with differences in detail. Before discussing the *Endomyaria* further, however, it will be well to try to get at the relationship of *Endomyaria* and *Mesomyaria* to other groups.

If it is fairly clear that both these groups originated somewhere near *Halcampa*, the same is still clearer of the *Athenaria*—i. e. the *Halcampids* themselves and their burrowing descendants. There is also a clear suggestion of origin from a *Halcampa*-like ancestor in the *Endocoelactaria*, and they must be thought of as *Halcampa*-stock diverging from the main lines. The *Stichodactylina* (excluding the *Corallimorphidae* and *Discosomidae*) are to be thought of as specialized *Endomyaria*. The first idea to establish then is that *Endomyaria*, *Mesomyaria*, *Endocoelactaria*, and *Athenaria* are the outcome along different lines of a *Halcampa*-stage with strong retractors and with ciliated tracts on the filaments. That is, they are 'post-*Halcampid*' and form a single class, *Nynantheae* s.s. as defined on pp. 540 and 552, and in Part III.

Next, there are the *Gonaetiniidae*, *Ptychodactidae*, and *Madreporaria* to be considered. The idea I hope to work out in connexion with these is that they originated in an ancestor earlier and less advanced than *Halcampa* (it would of course also give rise to *Halcampa* itself), and in fact may be called 'pre-*Halcampid*'.

What forms are more primitive than *Halcompa*? It was suggested in Part I that *Gonaetinia* and *Protanthea* are survivals of something very early (see pp. 493, 496-7, &c.). The grounds are these. The 'Halcompa-stage' in evolution may be defined as a stage with six pairs of perfect mesenteries (including two pairs of directives) bearing strong retractors, gonads, and filaments with ciliated tracts; any mesenteries beyond these six pairs would be rudimentary; there would probably be little or no base, a fairly narrow body, and little or no sphincter (cf. Text-figs. 8 and 7, c, d). This is not the Halcompa-stage sometimes used in an embryological sense, but is the way in which the term is usually taken for purposes of this paper. Now the Gonaetiniids have paired mesenteries, but not six pairs perfect—only the eight protocnemial couples are fully developed. The filaments have no ciliated lobes, and the mesenteries have very weak musculature, not forming retractors as in the Halcompa-stage. Moreover, the body-wall, tentacles, disc, and actinopharynx approximate to each other in structure, at least as regards ectodermal muscle, and mostly spirocysts. This gives something much nearer a possible ancestor for the groups not specified as post-Halcompid than anything else. The consideration of Anthozoa generally, suggests inevitably that mesenteries coupled before they paired, and the Gonaetiniids still keep a vestige of the coupling which *Halcompa* has lost (see Text-fig. 16, b)—and in a case like this the generalized musculature may be taken to indicate a stage before much differentiation of tentacles from body-wall, and of good retractors, had set in.

There seems no reason to think that the *Ptychodactidae* or *Madreporaria* ever passed through a Halcompa-stage in the sense outlined above. They did not attain to much in the retractor line, and the *Ptychodactids* did not differentiate the parts of their ectoderm very markedly. They never have ciliated tracts on the filaments, and their whole organization and histology, especially of course in *Madreporaria*, suggests a difference of direction in evolution from that of the post-Halcompids.

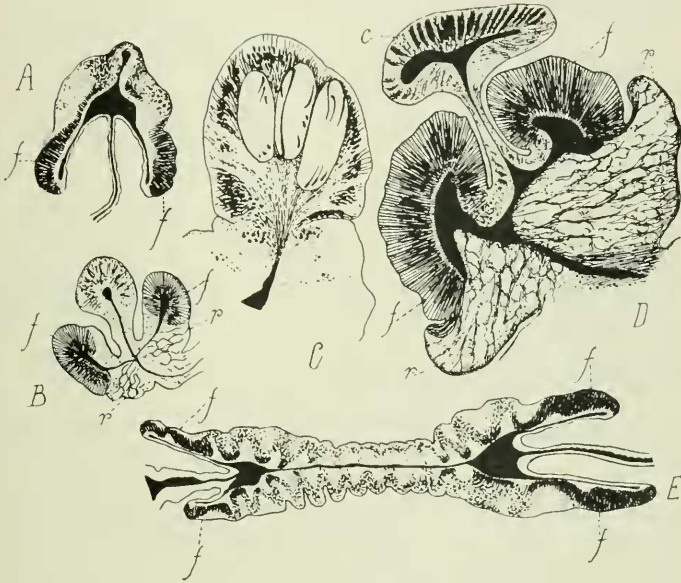
Although these forms (Gonactiniids, Ptychodactids, Madreporae) must be put down as pre-Halcaampid, they have common features establishing them as distinct from Edwardsiaria and Zoanthinaria, and they form one group, Dodecactiniaria—for instance, they have typically attained pairing of mesenteries and equality of directives, and the pairs are not usually formed each of a macro- and a micromesenteric partner, nor do they usually develop in two lateral zones of increase only, after a certain point; there are no canals in the body-wall save in some of the skeleton-making Madreporaria.

So that it may be said that the Dodecactiniaria present on the one hand descendants of a Gonactinia-like form, and these are poor in muscle and lack ciliated tracts; and on the other hand descendants of a Halcaampa-like form (itself, of course, the outcome of an earlier Gonactinia-like one), with the ciliated tracts stabilized and a tendency to muscularity.

Is the ancestor of the Zoanthactiniaria, the group containing the Dodecactiniaria as well as the Edwardsiaria and Zoanthinaria, simply the same sort of Gonactinia-like animal? The whole situation suggests that it must have had a good deal in common with Gonactinia—it would surely be a small form with weak muscle and generalized ectoderm and only eight perfect mesenteries (see Text-fig. 16, Δ); the chief point of debate is, had its filaments ciliated tracts? At first glance one would say No, the state without the tracts is more primitive; but there are other things which do not suggest that it was devoid of them. That the ancestor of all Anthozoa was without them seems certain, but that is even farther back than the one here visualized. Our Zoanthactinarian ancestor gave rise to Edwardsians and Zoanthids as well as to Dodecactiniaria, and both the former have ciliated tracts, even if they are not quite the same as those of the Nynantheae. This suggests that either (i) the Edwardsians and Zoanthids attained them independently, or else that (ii) the Gonactiniids, Ptychodactids, and Madreporaria lost them, while Halcaampa and its followers retained, stabilized, and developed them. (See Text-fig. 17 for the main types of filament here mentioned.)

The first assumption, of independent acquisition, would not be unreasonable, but at the same time it does seem likelier that the ancestor of all three had ciliated tracts, perhaps only in a slightly differentiated form; and it is a simpler way of putting things to think of some forms losing them than of

TEXT-FIG. 17.



Mesenterial filaments. A and E, a Zoanthid, with powerful ciliated tracts (*f*). E passes twice through these, as it cuts through a curved edge of mesentery. B, *Edwardsia*. Ciliated tracts present but less marked than in the Zoanthid; here and in D there are also reticular tracts (*r*). C, *Paradiscosoma*. Here there are no ciliated tracts, but three large sting-cells are shown. D, *Artemidactis*. Typical Actinian filament, with median endo-glandular tract (*c*) and lateral ciliated and reticular tracts.

three groups gaining them. There seems no special reason why such an ancestral form as that under consideration should not have weak ciliated tracts, because although very distinct structures they would easily be differentiated early on, just as acontia seem to have been at the *Eosagartia* stage in

the history of the Mesomyaria. It provides an idea parallel to that of loss of acontia by various forms, advocated in Part I.

I do not feel that the loss of ciliated tracts by some forms can be very fully accounted for, but it is easier to explain than their independent acquisition in three cases would be. The suggestion I should like to offer in this connexion was made to me by Professor Fleure, and does seem to make it intelligible. In certain Gastropods where the gill-lamellae are not much strengthened and kept apart skeletally, there is a device for keeping open chinks between them, for the passage of water, by means of pads of cilia. It is an attractive idea that part of the function of the anemone's ciliated tracts is something of the same sort—a preservation of chinks allowing access of water between the mesenteries, for respiratory purposes and so on. In the light of this several things may be noted. Among the forms with no ciliated tracts there is little or no sphincter, which means not much tight closing-up of the body. The forms with the tracts have above all developed strong retractors or sphincter, or both (with fairly numerous exceptions), and can often spend a good deal of time tightly shut up—in which condition, of course, the pads would function very well. The marked development of the tracts in Zoanthids fits in with this idea. Among the tractless forms the only really successful ones are the skeleton-making corals, and these have got over any difficulty by keeping their mesenteries apart with septa; and the other groups are seemingly quaint survivors, and some of them are so constituted that there is not much crowding in the coelenteron. It is not impossible that certain appearances in some of the filaments devoid of ciliated tracts represent vestiges of them; similar appearances may be present, it is true, in forms with the tracts—but even here they might be vestiges of the weak tracts of the ancestor which were superseded by much better ones. On the other side of the question it must not be forgotten that there are analogues of the ciliated tracts in Ceriantharia, but here again the ancestor may not have been far from that of the Zoanthactiniaria.

Summarizing so far, we get the suggestion of an evolutionary course somewhat as follows :

From a small, delicate, bilateral ancestor, with eight feebly muscular mesenteries, with some degree of differentiation of ciliated tracts, and with generalized ectoderm, there arose

- (i) *Edwardsiaria*, the mesenteries of which never paired, but some of them attained muscularity (see Text-fig. 16, E).
- (ii) *Zoanthinaria*, the mesenteries of which paired, but which went in for various curiosities (see Text-fig. 16, F).
- (iii) *Dodecaactinaria*, the mesenteries of which paired, and which developed along the familiar 'Hexactinian' lines.

There is just the possibility of an alternative view of the *Edwardsiaria* to the one adopted in this paper—namely, that they might somehow be *Nynantheae* in which certain mesenteries had been suppressed so that now there are only couples and not pairs. It is their histology which rather suggests *Nynanthean* affinities, but this idea is put forward very tentatively and further work would be required to ascertain how far it could be entertained as a possibility.

The *Dodecaactinaria* split on the rock of sluggishness versus muscularity.¹ The *Gonactinia*-like ancestors experimented a little, and gave rise to the *Gonactiniidae* and *Ptychodactidae*, perhaps trial-lines, on the one hand, and to the corals on the other; all these losing the ciliated tracts and never getting very muscular, the majority-forms going in for strict sedentarieness and skeleton-building, often colonially. In a different direction there arose from one of the *Gonactinia*-like ancestors a muscular *Halecampa*-form: this, far from losing the ciliated tracts, developed them further, and gave rise to the individualized and typically muscular forms, which fell into four sets—*Athenaria*, *Endocoelactaria*, *Mesomyaria*, *Endomyaria*.

¹ See in this connexion Chapter VIII in Thomson and Geddes, 'Evolution'.

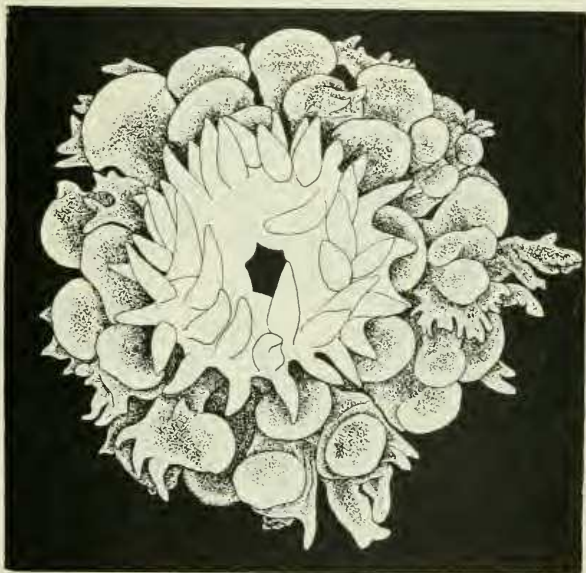
From this point evolution among the *Halcompa*-descendants or *Nynantheae* may be further considered.

About the *Athenaria* and *Endocoelactaria* little further need be said beyond what may be found in the special sections on those forms. The *Athenaria* are highly muscular as regards their mesenteries, this being useful in a burrowing existence. They have diverged among themselves in curious ways, and some of them present rather interesting special features, such as the immense siphonoglyphe and conchula of *Peachia* (presumably a development connected with drawing in a water-current when the animal is below the sand), and the knobbed tentacles of *Eloactis*. *Harenactis* has become very attenuated, with many cinclides—and indeed there are often cinclides among these forms. The *Endocoelactaria* are obviously divergent in another way. The earlier ones, most nearly represented by *Carlgrenia*, would be not far from the *Halcompa*-stage, but with secondary mesenteries (microcnemes at first) appearing in the lateral endocoels, and oriented like directives—this modifying the whole plan of structure. A stage further is represented by *Halcurias*, with ten pairs of macrocnemes instead of six, and later in the *Actinernids* the distinction into macro- and microcnemes has gone and numerous mesenteries are perfect, and often there are lobed discs, swollen tentacles, thick body-walls, and deep sea habitat. A sphincter never appears.

This leaves the main mass of forms, the *Meso-* and *Endomyaria* (including *Stichodactylines*). With regard to the justifiability of these two groups, if the work of this paper and of Part I be taken into consideration it should emerge that so far as we can know anything about these things, the *Endomyaria* did, as a bunch, follow a different line of tendency from the *Mesomyaria*, and if that is established the grouping follows. It is mainly a difference of tendency, there being, at any rate low down in the two groups, probably no essential histological difference—this might come in higher up, perhaps, in comparing such forms as *Actinosecyphia* and *Catadio-mene* with *Thalassianthus*.

Among the Endomyaria the sphincter, if present, is endodermal. There are never any acontia. After early evolutionary stages are past, there are often vesicles, sometimes very complex ones, on the body; verrucae and acrorhagi are frequent; and in some cases the tentacles increase in number or become

TEXT-FIG. 18.

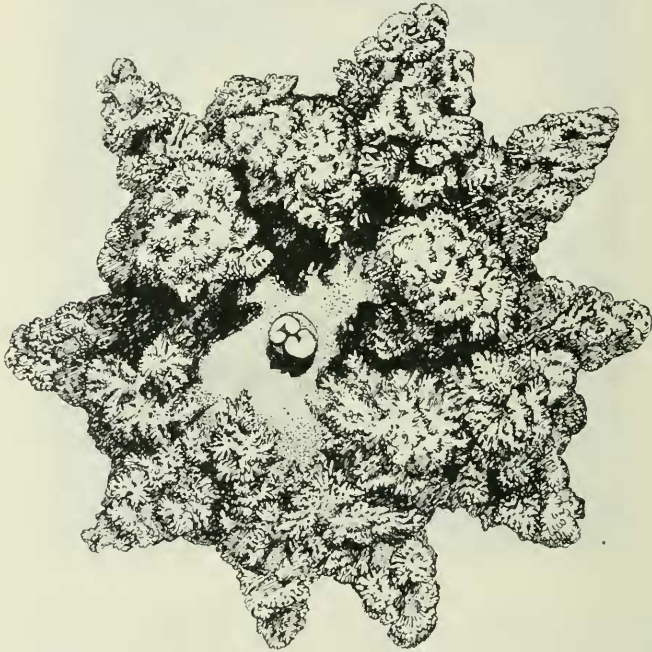


An enlarged view, from above, of a whole specimen of *Phyllo-discus indicus*. The tentacles are not shaded, and form the central part, and projecting beyond them is the corona or ruff of compound vesicles. An example of complexity affecting outgrowths of the body.

curiously modified in form—vesicular or branched, sometimes quite feathery in their subdivision. There is little or no tendency to thicken body-walls of the sort found among Mesomyaria, and never are there basal mesogloal swellings to the tentacles. The tentacular musculature rarely becomes mesogloal. A definite base has been attained save in one case, and typically there are basilar muscles. The secondary

mesenteries appear in exocoels, and usually the musculature of the body-wall ectoderm is lost. The habitat of the forms with vesicles and elaborate tentacles is often tropical. Text-fig. 18 gives a good example of one of the forms with a frill of vesicles. The crown of tentacles (unshaded) is seen to be surrounded by a wider corona of compound vesicles, like a ruff,

TEXT-FIG. 19.



Actinodendron plumosum, copied from a photograph of a living specimen by W. Saville-Kent. See acknowledgement on p. 496. An example of complexity affecting tentacles and disc.

projecting beyond it. A vertical section of the same form is shown in Text-fig. 2, A. A case in which the tentacles are dendritic and form a frill, being borne on permanent arm-like projections of the disc, is shown in Text-fig. 19, and other variations in Text-figs. 14 (tentacles) and 1 (acrorhagi).

In Mesomyaria, on the other hand, we get the sphincter,

when present, mesogloea. Acontia are often present. Real vesicles or frilled tentacles do not occur (the tentacles are slightly complicated in one or two cases), nor do acrorhagi; there is never more than one tentacle to an endocoel (often there are more in Endomyaria, and it may be so on the exocoels also), and the tentacles often have a thick basal mesogloea swelling aborally. Thick body-walls and knobs and crests of mesogloea are fairly frequent (see Part I, Text-figs. 24, 25, 26, 27, 31). Tentacular musculature is more often mesogloea than in Endomyaria.

Possibly the acontia in the second group, the acrorhagi and vesicles and complex tentacles in the first, are different expressions of stinging tendencies along different lines, going with the sphincter-difference and so on, the frills especially associated with warmer seas, the curiosities of the Mesomyaria often connected with deep water. One difference is that acontia seem to have been ancestral in the Mesomyaria and to have been lost in certain cases; whereas vesicles and such things must be the attainments of certain individual sets of animals at given points.

Lastly, evolution within Endomyaria may be a little more closely thought of. For Mesomyaria see Part I.

The general direction has been decided on (see p. 554). The simplest way will be to put the route suggested by the facts as narrative, as before, and it must have been something more or less like the following:

From an Eoactinia (near to Eosagartia—see Part I) or Halcampa-like form with little or no base, no sphincter, and six pairs of macrocnemes and a few microcnemes, at first one line of evolution only started.

An adherent base was gained, at first, and an increase in the number of tentacles and microcnemes, but nothing else (cf. Text-figs. 8 and 16, c). There are survivors of this stage even now, the Condylanthidae.

Next, the distinction between macro- and microcnemes was lost, but at first only the former macrocnemes remained perfect (cf. Text-fig. 16, d). Some forms began to get an endodermal

sphincter, though not a very strong one; some developed suckers on the body-wall, and one curious animal formed special sphincters whereby it could cut off its tentacles at will—it also retained some primitive features (*Bolocerooides*). The present-day forms which have gone no further than this are the *Myonanthidae*.

A large number of forms, however, did go further, and attained a larger number of perfect mesenteries (cf. Text-figs. 16, II, and 10). Often the endodermal sphincter developed and sometimes became very strong, though some forms still remained sphincterless, or with very little or a moderate sphincter. Some of the advanced ones with strong sphincters have the tentacular and discal musculature embedded in the mesogloea. Among these forms the body either remained smooth, or developed verrucae or acrorhagi or both, but never vesicles. These are the *Actiniidae* s.s. in the sense taken on p. 546.

To go back a little, from somewhere near the *Myonanthidae* arose a group of delicate forms which retained the six pairs of perfect mesenteries, but the body became divided into a scapus and capitulum, and either from the scapus or from the region where scapus and capitulum join (and sometimes above that region as well) there grew out hollow sac-like diverticula, often compound—the vesicles. Little or no sphincter was attained. These forms are the *Aliciidae*.

There is another set of forms with these vesicles, but with usually more numerous perfect mesenteries. They sometimes have a less delicate body, and occasionally mesogloal tentacle-muscle. There is often a well-developed endodermal sphincter, but it may be weak or absent. Perhaps these, or some of them, arose, independently of the *Aliciidae*, from among the *Actiniidae*, or perhaps they arose from near the *Aliciidae* by a mesenterial change. Whichever way it was, they represent onward steps. They are the *Phyllactidae*—a somewhat heterogeneous group to be further discussed in Part III. A section of one of them, with many perfect mesenteries, is shown in Text-fig. 10.

A form, or perhaps several forms, which from our hitherto incomplete knowledge of them would seem to have arisen near

the Actiniidae, took to a floating life, swimming upside down. The base developed into a regular float, and certain anatomical peculiarities appeared. These are the Minyadidae.

Other advanced stages are represented by the various families of 'Stichodactylines'. These arose from some Actiniid or pre-Actiniid ancestors, and they have usually the numerous perfect mesenteries, and often endodermal sphincters, which may be quite strong. The sphincter is endodermal or absent, never mesogloal. Among themselves they diverged into seven families, easily distinguished from one another. The differences affected the arrangement of the tentacles on the endocoels and exocoels, and their form—they might be simple, pinnate, dendritic, sessile and vesicular, feathery, modified into special stinging 'nematospheres', and so on. The other part of the structure chiefly affected by variation was the musculature—there might be absence of sphincter in one case compensated for by strong retractors; or very strong sphincter and retractors but poor tentacles; and so on.

It will be seen from the above outline, and from that given earlier for Mesomyaria, that there is one thing assumed as having independently taken place in Endomyaria, Mesomyaria, and Endocoelactaria—and possibly more than once in Endomyaria: that is, that in each of these cases a start was made from the condition in which the mesenteries are divided into macro- and microcnemes, this was lost, and in the end there were graded mesenteries and numerous perfect pairs. This is, however, a convergence quite to be expected among forms making in a general way towards increase of size and diameter of the individual, and correlated multiplication of organs. Whatever arrangement be adopted, there is some convergence cropping up, but when one thinks of the vertebrate and cephalopod eye, or of the Marsupial and ordinary wolf, a convergence like that assumed here seems very simple.

In the two hypothetical ancestors of Endomyaria and Mesomyaria (*Eoactinia* and *Eosagartia*) there is no harm in assuming for them ectodermal muscle in the body-wall, and the same may probably be said for the *Eoactinia*-like

ancestors of Athenaria and Endocoelactaria. This would allow for the retention of the musculature, or of traces of it, here and there, with a dominating loss of it along all the lines.

6. SUMMARY.

It is difficult to make a concise summary of a paper covering a good many inter-related discussions, but the following is an attempt to give some of the main points with reasonable brevity.

1. There is difficulty in defining specificity among Actiniaria, as in other lowly and plastic animals. Among British forms species are well enough marked on the whole, if studied alive so that colour and habit can be taken into account. When preserved, however, too little is known of possible range of specific variation in anatomy for much to be done. Foreign forms are so often known in death only that species are somewhat in chaos and there is little firm ground. Experience leads one to the view that among these low and plastic forms a species may have its peculiarities of organic constitution at an early stage of the development of their expression, such expression having affected colour-scheme and general facies of the living animal but not necessarily to any extent the internal anatomy which can be studied in preserved specimens. Much work needs doing by way of studying all forms alive, and of killing and preserving numerous individuals which belong certainly to the same species, in different ways, and studying them so as to reveal effect of reagents, age, state of contraction or distension, locality, reproductive maturity, and so on, on the anatomy. When a better knowledge of the limits of specific variation is gained (and they will be much wider in some species than in others) a revision of species might be attempted. Especially the value or otherwise of measurements of nematocysts as specific characters should be looked into.

2. Although species are in a poor way, genera and families are on the whole much easier to understand and make use of, and here there are enough data to start a methodical classification

with. Omitting for the sake of brevity any criticism of existing classifications, and regarding Actinaria as an unclassified series, it may then be inquired what method can be applied to them to find out their inter-relations. Clearly unit characters are not much help, since they may vary independently, and may enter into combination in different genera with various sets of others. It is therefore necessary to sum up the chief features of each genus, and to see which genera have most in common with which others; and those sharing most can be united in families. The result is a natural grouping, and one which expresses relationships of animals as wholes, and not analogies of isolated parts of their bodies. The classifications of Lamellibranch Mollusca may be referred to as an example of several overlapping schemes affecting the same group, founded on few characters, and each expressing the relationships and evolution of one set of anatomical details (be it siphons and pallial lines, hinge lines and teeth, adductor muscles, or gills), and not expressing those of Lamellibranch animals as wholes.

It is found, however, that after applying the method of summation of characters, families can be defined by half a dozen or more common features, and may form so graded a series that there are only unit-differences between some of them. On the other basis there were sometimes only single or few differential resemblances between the members of a family, accompanied by important differences. To look at it from another angle, it has been said that criticism is finding out why one likes or does not like a given book or picture. It seems fair to say that classification is finding out why a horse is more like a mule than like a wolf—we know instinctively that it is so, but if we can confirm that instinct by good reasons we have a classification. Similarly, given enough study of a group, and enough training of the relationship-instinct, it is felt that from their whole organism and make-up certain forms are more nearly related to some of their brethren than to others. This may be of very great help, but of course needs cautious exercise and confirmation. The point is that the principle of summation of chief characters gives this

confirmation in a way that an artificial system of unit-characters cannot do—it justifies and bears out the instinct. The summation principle also enables the family to be used definitely as the expression of a step in the evolution of any set of forms, and the classification represents evolution of whole anemones, not of their sphincters or tentacles only. It also provides evolutionary hints which could not otherwise come to light, and which, given a general idea of group-evolution, help to confirm and enlarge it. The general idea itself can grow from a comparison of early and advanced forms, embryology, and so on. From working through a whole group in such a way it does seem possible to get a glimpse of the rhythmical development of the life in the creatures, expressing itself in the various ways at its disposal and unfolding along various lines. It should be noted that in dealing with a group as plastic as Actiniaria, it is often necessary to define differentiation of tendency without too much insistence on hard and fast divisions without qualification or exception.

3. The classification worked out on the above lines, in this paper, is as follows. For definitions of the groups and families, and for limitation of the sense in which they are taken, reference should be made to the portions of the paper where these things are dealt with. I have accepted the arrangements of Bourne and Carlgren as regards sub-classes of Anthozoa; and that of Bourne for orders and sub-orders. The tribes, sub-tribes, families, and genera have, however, been largely revised in this paper. I have kept as near to Carlgren's tribes and sub-tribes as I felt possible, and have throughout used old names where I could; but the sense of his groups has been altered and they have been added to, and many of the families more narrowly limited, so that the old names take on a new meaning.

CLASS ANTHOZOA.

- | | |
|---|--------------------------------|
| { | Sub-class 1. CERANTIPATHARIA. |
| | Sub-class 2. OCTACTINIARIA. |
| | Sub-class 3. ZOANTHACTINIARIA. |

Order A. Edwardsiaria.

Order B. Zoanthinaria.

Order C. Dodecaetiniaria.

(Sub-order (i) MADREPORARIA.

(Sub-order (ii) ACTINIARIA.

Tribe a. Protantheae.

Tribe b. Ptychodacteae.

Tribe c. Nynantheae.

{	Sub-tribe <i>a.</i> Athenaria.
	Sub-tribe <i>β.</i> Endocoelactaria.
	Sub-tribe <i>γ.</i> Mesomyaria.
	Sub-tribe <i>δ.</i> Endomyaria.

The families will be found listed under their respective group on p. 542.

4. An idea of the evolutionary history of the group has been worked out in connexion with the above classification, and may be summarized as follows.

It is possible to guess at a small plankton swimmer with eight tentacles and eight mesenteries, without much definiteness of musculature, and with bilateral symmetry, and contrasting with, not resembling, the cruciform Scyphistoma, which must have been quite an independent outcome of a Hydrozoan. This small creature would give rise to several types much like itself but with differences of detail, each of which would give rise to a main Anthozoan sub-class. Only the one which gave origin to the Zoantheactiniaria need be followed here. This stock seemingly shed out curiosities at first: some of them took to burrowing and life in cracks, and became vermiform, but did not amount to much (Edwardsiaria); others went in for colonialism and incrustation and had fair success in a coral-like way (Zoanthinaria). The main line, however, divided fairly early into two great groups, the split being upon the rock of sluggishness and colonialism and skeleton-building versus comparative activity, specialization of the individual, greater muscularity, and no skeleton. The two groups are of course corals (Madreporaria) and sea-anemones (Actiniaria). There are a few corals which developed no skeleton, or else lost their skeleton, and which though often simple show colonial tendencies.

They have usually been classed with the anemones, but it appears that they are almost identical in structure with coral-polyps, but unlike anemones. Their lack of skeleton cannot keep them out of Madreporaria, and the transference makes the division between the two groups, as regards soft parts, more intelligible. They are the Corallimorphidae and Discosomidae.

Returning to the sea-anemones proper, they seem first to have experimented with further curiosities, which perhaps diverged from the main stock about the same time as the corals, or a little later. These experimental forms fall into two sets, with a good deal that is primitive about them, one of them resembling as nearly as any surviving form the supposed ancestor of the whole Zoanthactiniaria. They are the Proanthaeae (Gonactiniidae) and Ptychodacteae. After this the main line attained a definitely muscular *Halcampa*-like stage with well-marked ciliated tracts on its mesenterial filaments, and from this point two main lines of divergence may be traced, and two lesser lines. Of the subsidiaries, one group (Athenaria) took to, or simply remained in, a burrowing life, and retained a good deal of simplicity; the other (Endocoelactaria) went off in a curious direction, the reverse of that taken by most forms, as regards some details of its mesenteries, and possibly gives a clue to the origin of Tetracorallia. This group shows one tendency in common with the two main lines to be next dealt with—a general move towards increase in size of the individual, especially in diameter, and increase in the number of effective organs; with musculature tending to change from a few strong retractors on a few mesenteries to a larger number of less specialized ones.

The two main lines both went in for development of a marginal sphincter, but otherwise their differences of tendency are marked. The Mesomyaria developed mesogloecal sphincters, and these, when they have special stinging organs, have acontia, never or hardly ever acrorhagi or frills. And although diverging among themselves, many of them tend after a time to take to deep-water life. In correlation with this they may

lose their acontia and may lose mobility, and develop stiff or thick body-walls, their metabolism slowing down and spare energy sometimes being used up in the production of knobs and crests and solid horn-like tentacular swellings. This is a tendency towards fixity of character and possibly thence towards ultimate extinction. It is interesting to note that some of the above-mentioned Endocoelactaria have reached a similar state, although along an entirely different line.

The other main line, Endomyaria, went in for endodermal sphincters if any, and their special stinging organs are never acontia, but they often have acrorhagi and other things. Some of them develop vesicular blisters and compound acrorhagi which may reach wonderful complexity of structure; in others the tentacles increase in number and sometimes they, not the outgrowths of the body, become complex, at their finest with a frill-like effect. These forms, whether it be body or tentacles that complexify, are more especially found in the warmer seas, and here the tendency to fixity of character does not seem much indicated. Along both lines various forms halted by the way, of course.

This idea of the evolution of the group may be helped out by the diagram printed below.

A more detailed outline of the history of Mesomyaria has been worked out, and will be found in Part I, p. 498, &c.; a corresponding one for Endemyaria is given in this part, p. 563, &c.

5. Apart from the above considerations, it has been the object of the paper to revise and re-define all the families and genera, sorting them out in such a way as to make them as homogeneous as possible, and to represent their relationships naturally, with the idea of getting the definitions as precise as is feasible in order to facilitate identification. It has the advantage of collecting all the definitions together, but at the same time is not meant to be an exhaustive compilation as regards species-lists and so on. Only a minimum of synonymy is included, and insufficiently known forms are left alone. The classification worked out is, admittedly, complicated rather

than simple, but that is inevitable in a large and very old group.

6. It seems fair to suggest that the principles advocated and put into practice here might with advantage be applied to other animal groups (e.g. Gastropods and Lamellibranchs). It is not for a moment implied that the classification of animals as at present understood does not group them correctly, speaking broadly and of the main groups; but that it needs revision and supplementing on the plan suggested, especially in the cases of some of the sub-groups, the classification of which sometimes seems tentative and not very clear. It appears that nearly enough data are now collected about animals to permit of entry on a new phase in the history of classification. It is becoming evident, with regard to species for instance, that some new system will shortly have to be devised which will more adequately represent their inter-relations, and allow for the idea of interlacing systems of concentric circles with the characters of the central individual in each system as those of the species, which has grown up. Some new conception will probably work itself out about classification in general also, and the revision of some groups in accordance with ideas advocated here is suggested as a small beginning along the road—a beginning which may possibly lead to further steps in the realization of the new conception. If it prove to be a blind alley, that conclusion should not take very long to emerge.

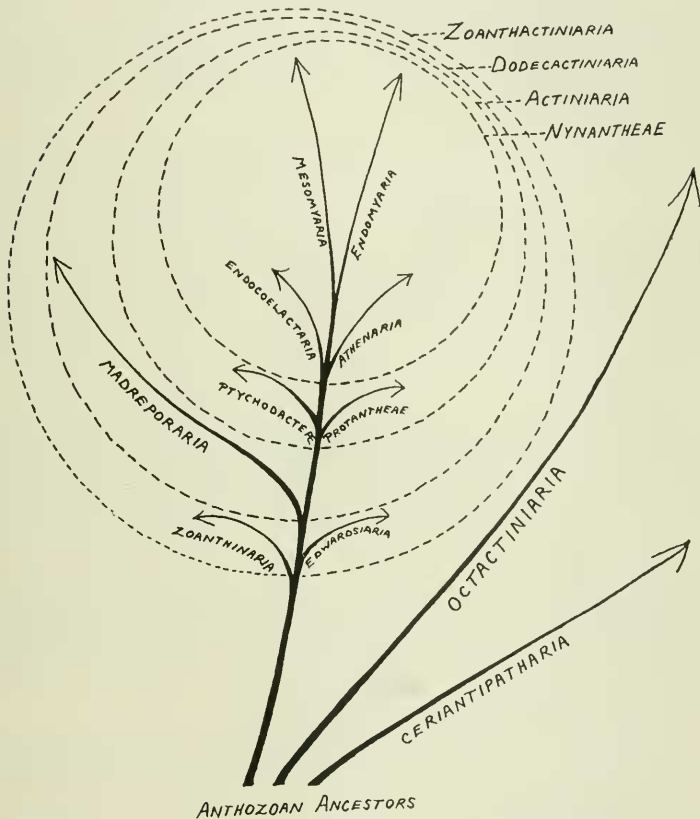
7. SHORT GLOSSARY.

This is not in any way a complete glossary, but is meant for use in connexion with a few terms which more than most seem to require definition, for convenience in using the paper.

ACONTIA.—Slender white or coloured threads attached to the borders of the mesenteries in some families of Actiniaria, just below the mesenterial filaments. They are loaded with nematocysts, and can be protruded through the mouth, and in some cases also (accidentally) through pores (cinclides) in the body-wall, for purposes of defence or to paralyse prey. Histologically they differ from mesenterial filaments.

ACRORHAGI.—Marginal outgrowths of the body-wall found in some genera of Actiniaria, and which may or may not be specialized as nematocyst-batteries. They may be simple (spherical, conical, &c.), slightly compound, or even frondose.

TEXT-FIG. 20.



Diagrammatic representation of the classification and evolution of the Zoanthactiniaria.

CAPITULUM.—The bodies of some Actiniaria show a distinction into three regions: the main part of the body in such cases is termed the scapus, and may be provided with cuticle. The distal extremity, which bears the tentacles, is

termed the capitulum; it may or may not be very distinct from the scapus; usually it has no cuticle; it may be delicate and different in structure from the scapus, and introvertible into the latter. The aboral end of the body if rounded and able to become bladder-like is called a physa. Some adherent forms possess scapus and capitulum, but ordinary base instead of physa; among these the capitulum may be delicate or may be very thick-walled. There are grades between a physa and a well-marked adherent base, and some bases may temporarily become physa-like.

CILIATED TRACTS (*Flimmerstreifen*) of mesenterial filaments. In the filaments of *Zoanthinaria*, *Edwardsiaria*, and *Nynantheae*, a transverse section cut at the right level will show a trifoliate outline, portions of the lateral lobes of the trefoil being composed of plain ciliated cells, these portions forming, therefore, in the whole filament, lateral ciliated tracts on either side of a median glandular or cnidoglandular tract (*Nesselldrüsenstreif*).

CINCLIDES.—Pores in an Actinian body-wall. Function perhaps connected with water-currents; in some cases they seem to provide safety-valves against rupture of the wall on sudden jerky contraction. Connexion with acontia secondary and indirect.

CONCHULA.—The specialized upper extremity of the siphonoglyphe in the genus *Peachia*. Perhaps connected with the entry or exit of a water-current when the animal is embedded in sand up to the disc.

COUPLE of mesenteries. See foot-note.

ENDOCOEL. The space between two mesenteries of the same pair.¹

¹ In this paper the word 'pair' is used of two mesenteries, both on the same side of the body, and adjacent to one another—and usually with their retractor muscles *vis-à-vis*. The word 'couple' is applied to two mesenteries arising at the same time and symmetrical about the long axis of the actinopharynx, but one on one side of the latter, and one on the other; their retractors facing the same way. Thus ordinary directive mesenteries are strictly couples, though usually called pairs for convenience.

EXOCOEL.—The space between two pairs of mesenteries.

FOSSE.—Some anemones have the margin of the body raised into a distinct rim or parapet, outside the bases of the tentacles; the circular groove between this parapet and the tentacle-bases is known as a fosse.

MACROCNEME.—A typical macrocneme is a well-developed mesentery which joins the actinopharynx as well as the body-wall, has a strong and usually circumscribed retractor muscle, a gonad, and a mesenterial filament. There are sometimes variations in detail from this general plan.

METACNEME.—Any mesentery formed after the earliest eight mesenteries to appear (protocnemes).

MICROCNEME.—Typically a narrow mesentery which does not join the actinopharynx, has little or no muscle beyond a 'parietal muscle'—no retractor therefore—no gonad, and no filament. Variations from this typical scheme are found, however.

NEMATOSPHERE.—A tentacle which has become converted into a short structure rounded at the end, or into a practically sessile sphere, and the ectoderm of at least part of which is crowded with nematocysts.

PAIR of mesenteries. See foot-note on previous page.

PERFECT MESENTERY.—In a form where there are graded cycles of mesenteries (i. e. no division of the mesenteries into macro- and microcnemes), any mesentery which joins the actinopharynx as well as being inserted into body-wall and oral disc, is termed 'perfect'. In a form where there are macro- and microcnemes, the former are of course 'perfect' as part of their macrocnemic nature; but in some cases some of the microcnemes may join the actinopharynx though otherwise more or less rudimentary. They are then technically 'perfect' mesenteries, but are by no means macrocnemes. In the forms with graded cycles, the perfect mesenteries have filaments and retractors, but not always gonads, which in such forms may appear on the 'imperfect' mesenteries only. In such forms the older imperfect mesenteries, at least, may have retractor, gonad, and filament, so that they are not

microcnemes although less fully formed than the perfect mesenteries.

PHYSA.—See Capitulum.

PROTOCNEME.—The first four bilateral couples¹ of mesenteries to be formed in a Zoanthactinarian.

SCAPUS.—See Capitulum.

SPHINCTER.—The sphincter usually referred to in this paper is the one running round within the upper margin of the body, outside the tentacle-bases, in many anemones. It may be embedded in the mesogloea of this region (mesogloea), or its fibres may be supported on processes of mesogloea which project into the endoderm (endodermal). It may be spread out a good deal (diffuse) or gathered up into a definite sharply marked-off cord, which at its best forms a marked projection from the body-wall into the coelenteron (circumscribed). There are various intermediate grades between diffuse and circumscribed, and various degrees of strength in sphincters.

STICHODACTYLINE condition of tentacles. This is the term used to denote the state of affairs in which more than one tentacle communicates with at least some of the endocoels, sometimes with all endocoels, and with exocoels also.

VERRUCAE.—These are local, slightly differentiated sucker-like warts or slightly hollow outgrowths of the body-wall, and often they attach foreign bodies to themselves.

VESICLES.—These are truly hollow, bladder-like extensions of the coelenteron into outgrowths of the body. They may be delicate and thin-walled, simple or compound, and some times are well provided with nematocysts.

¹ See foot-note on p. 574